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PLANKTON ECOLOGY OF THE RIVER HOOGHLY AT PALTA, WEST BENGAL[1]

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INTRODUCTION

The present paper gives a detailed account of studies on the periodicity and ecology of the plankton-flora and -fauna of the River Hooghly at Palta, about fourteen miles above Calcutta, over a period of three years from July, 1945, to June, 1948.

These studies were carried out in the course of investigation into the causes of interference with the normal working of filter beds of the Calcutta Water Supply during spring-summer and fall-winter, every year, when invasion of the filtering medium by profuse growth of micro-algae, especially diatoms, becomes a problem. To my knowledge, there have been no reports on the microscopic ecology of any river in India.

METHODS

The River Hooghly water is too turbid during most of the year for even directly viewing a depth of one millimeter of it through the microscope, as is required by methods such as that of Sedgwick-Rafter (1888). Turbidity also makes methods of concentration like filtration, centrifuging, etc., practically useless. So, a simple modification of Lackey's method (1938) was adopted for plankton estimation.

The samples of water were collected in one-litre bottles from off shore daily at 7 A.M. After uniformly and gently shaking the bottle, one drop of the water was mounted under a cover glass of 20 m.m. width from a 1 c.c. pipette delivering 14 drops of water per c.c., so that the water spread uniformly under the cover glass, the whole system forming a square-block. The organisms in the two paths passing at right angles through the centre of this block were counted with the combination 10 X and 12 X eye-piece, giving a field of view of 1.4 m.m. diameter. The counts were made in terms of Whipple's Areal Standard Units (1927) and repeated five times with five drops of water separately. The mean of the five readings was multiplied by 100 to get the number of Areal Standard Units of the organisms per c.c. of water (A.S.U./c.c.). The weekly average counts were obtained from the daily estimations.

The physical and chemical analyses were made according to standard methods (Amer. Pub. Health Assoc. and Amer. Water Works Assoc. 1936) as follows: Temperature was noted on the spot by an ordinary mercury thermometer in °C. Rainfall was recorded in inches. Turbidity was estimated as SiO_2 by the "Turbidity-Rod" method, salinity as –Cl by Mohr's method, alkalinity as $CaCO_3$ by titration with standard acid against methyl orange, hardness as $CaCO_3$ by castile-soap method, pH colorimetrically with phenol red, free-ammonia as N by Nesslerisation of the distillate from 250 c.c. of the sample and comparison with standard disc-comparator, albuminoid-ammonia as N by Wanklyn's process, nitrite as N by Illosvay's method, nitrate as N by phenol-disulphonic-acid method, dissolved oxygen by Winkler's method, and oxygen consumption by Tidy's process. The results were expressed in p.p.m. The phosphate ($-PO_4$) and silicate (SiO_2) values, as cited from past chemical survey records, had been estimated by stannous chloride and molybdate methods, respectively. The factors other than the nitrogen fractions, hardness, dissolved oxygen, and oxygen consumption were estimated daily and the weekly averages calculated from these daily readings. The latter factors were estimated weekly.

The annual averages of all estimations were obtained from the mean calculation of the monthly averages for the twelve months from July of one year to June of the next.

The Crustacea were excluded from this study because the method of sampling was considered inadequate for this group. The plankton identifications were made with the help of standard keys.

[1] This is part of a paper read and discussed at the Indian Science Congress, 1949 (Proc. 36th I.S.C., Part III, Abstracts, p. 147).

[2] I wish to acknowledge that the late Dr. M. U. Ahmed, Health Officer, and Dr. S. K. Ghosh, Chief Analyst, Calcutta Corporation, provided facilities for this study.

FIG. 1. Map of the River Hooghly, West Bengal, showing the major tributaries and the sampling station at Palta. The thick line indicates the boundary of West Bengal, beyond which lie the bordering states and countries.

The unidentified genera were discussed in the ecological considerations section. All the unidentified Flagellates and Ciliates are there included in the Protozoa. The Myxophyceae are included with the Schizomycetes in the Schizophyta of Engler.

The eleven diatom genera, *Cyclotella, Stephanodiscus, Fragillaria, Stauroneis, Pleurosigma, Gomphonema, Cymbella, Encyonema, Rhopalodia, Bacillaria,* and *Surirella,* are treated together under the heading "Remaining Diatoms" under ecological considerations, as their yields do not warrant separate consideration.

Hydrography of the River Hooghly

The Hooghly is the estuary of three different rivers, *viz.,* the Bhagirathi, Jalangi, and Mathabhanga, all of which come out of the Ganges and ultimately combine, the Jalangi meeting the Bhagirathi somewhere near Nabadwip and the Mathabhanga meeting the combined flow of these two somewhere near Ranaghat (Fig. 1). The Bhagirathi, the most important river of West Bengal, was the main course of the Ganges in the past, but has died out subsequently. As a result, the flow of the River Hooghly is also much reduced.

The Bhagirathi comes out of the Ganges at Dhulian. It drains all the territories situated on both its banks in West Bengal. All the rivers of Santal Parganas and Chotanagpur, viz., Bansle, Brahmani, Dwarka, Maurakshi, Kopai, Ajoy, Damodar, Rupnarayan, Sillai, Kasai, and Haldi, swell up in the rainy season, when they pour their monsoon waters (southwestern monsoon) into the Bhagirathi and the Hooghly. But the large volume of water brought into the River Hooghly during this time also carries down huge quantities of sand and silt. Tides flooding and ebbing from the sea twice a day, favoured by the much reduced river flow, cause a major fraction of them to be deposited on the river bed.

Like the hilly streams of Chotanagur and Santal Parganas, the currents of Bhagirathi, Jalangi, and Mathabhanga diminish and ultimately cease at the end of the flood season. The mouths of these rivers from the Ganges also are gradually becoming silted up, and as a consequence the Ganges water cannot enter into these rivers except during the rainy season. Hence, there is no other flow in the River Hooghly at the end of the rainy season but the flood and ebb-tides from the sea.

The level of water rises and falls with the tides, every day, through about a metre during winter and four metres during monsoon, making the average height of the water column to be ten metres approximately at the sampling spot.

Seasonal and Annual Variations of Yield of the River Hooghly Plankton

The seasonal variations in plankton yield are shown in Figure 2, curves A-F. The zooplankton constituted mainly by the Protozoa (*viz., Diffu-*

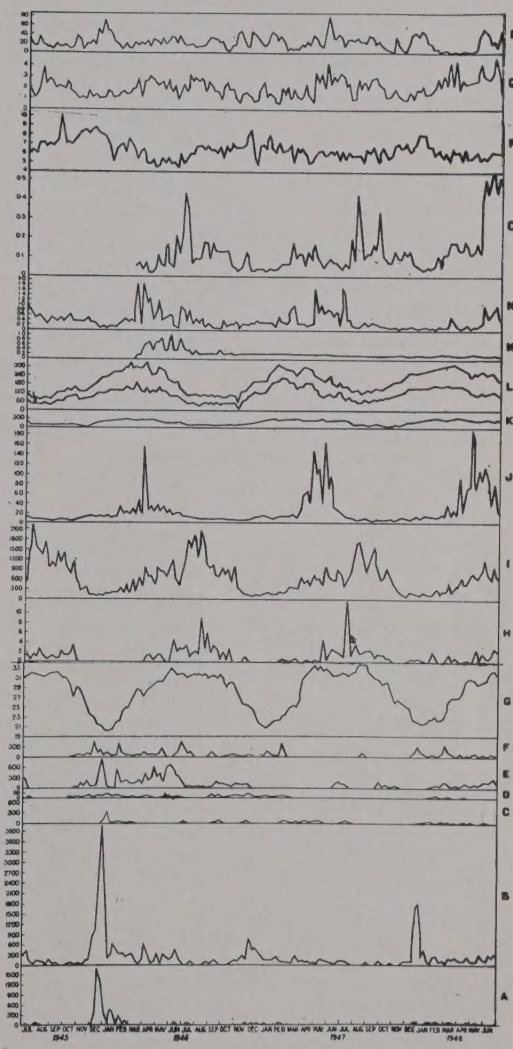

Fig. 2. Curves A, B, C, D, E, F show the seasonal variations of yield of Chlorophyceae, Diatomaceae, Dinophyceae, Euglenineae, Schizophyta, and Protozoa respectively; G, H, I, J, K, L, M, N, O, P, Q show seasonal variations of temperature, rainfall, turbidity, salinity, alkalinity, hardness (1. total, 2. temporary), free-ammonia N, albuminoid N, nitrate N, dissolved-oxygen, and oxygen-consumption respectively; and R shows seasonal variations of percentage of filtration-interference. One division of the ordinate scale represents 300 A.S.U./c.c. in A to F, 2°C. in G, 2″ in H, 300 p.p.m. in I and K, 20 p.p.m. in J, 60 p.p.m. in L, 0.2 p.p.m. in M and N, 0.1 p.p.m. in O, 1 p.p.m. in P and Q, and 20% in R.

TABLE I. *Genera observed, with time, frequency, and abundance indicated.*
The associated symbols Spr(spring), S(summer), F(fall), and W(winter) indicate periods of maximum occurrence; f(rare), ff(occasional), fff(frequent) indicate frequencies of occurrence; and + (insignificant), ++ (minor), +++ (major) indicate relative abundances as components of respective family communities. The species identified are within parentheses.

Family	Genus	Family	Genus
Chlorophyceae	*Pediastrum* Sff+ (*P. duplex* Meyen; *P. boryanum* (Turp.) Menegh.)	Diatomaceae (*Cont.*)	*Stauroneis* sp. Wff+
	Micractinium sp. Sff+		*Pleurosigma* sp. Wf+
	Tetraedron Sff+ (*T. regulare* Kutz.)		*Gomphonema* Wf+ (*G. constrictum* Ehrb.)
	Ankistrodesmus Sff++ (*A. falcatus* (Cordi) Ralfs; *A. setigerus* (Schrod.) G. S. West)		*Cymbella* Wff+ (*C. lanceolata* (Ehrenb.) Van Heurck)
	Actinastrum Sff+ (*A. hantzschii* Lagerh.)		*Encyonema* sp. Wff+
	Crucigenia Sff+ (*C. rectangularis* (Naeg.) Gay)		*Rhopalodia* Wff+ (*R. gibba* (Ehrenb.) Mull)
	Scenedesmus Sff++ (*S. quadricauda* (Turp) Brebisson)		*Bacillaria* Wf+ (*B. paradoxa* Gmel)
	Penium Sff+ (*P. libellula* Nordst.)		*Surirella* sp. Wff+
	Closterium Sff+ (*C. leibleinii* Kutz; *C. parvulum* Naeg; *C. monoliferum* (Bory.) Ehrb.; *C. rostratum* Ehrb.)	Dinophyceae	*Peridinium* sp. Wfff+++
	Cosmarium Sff+ (*C. granatum* Breb.)		*Glenodinium* sp. Wfff+++
	Geminella Wfff+++ (*G. interrupta* Turp.)	Euglenineae	*Euglena* Wfff+++ (*E. viridis* Ehrenb.; *E. acus* Ehrenb.)
Diatomaceae	*Melosira* Wfff+++ to + (*M. varians* Ag.)		*Phacus* sp. Wfff+++
	Coscinodiscus W to Spr fff+ to +++ (*C. radiatus* Ehrb.)		*Trachelomonas* sp. Wff++
	Synedra Wfff++ (*S. ulna* (Nitzsch) Ehrenb.; *S. pulchella* Kutz.; *S. affinis* Kutz.)		*Ascoglena* sp. Wff+
	Navicula Wff++ (*N. viridis* Kutz.)	Myxophyceae	*Oscillatoria* F and S fff+++ (*O. pseudogeminata* G. Schmid; *O. agardhii* Gom.)
	Nitzschia Wfff++ to +++ (*N. acicularis* W. Sm.; *N. linearis* W. Sm.)		*Anabaena* Wff+++ (*A. flos-aquae* (Lyngb.) Breb.; *A. circinalis* (Kutz.) Hansg.)
	Cyclotella Wff+ (*C. operculata* Kutz.)		*Aphanizomenon* Wff++ (*A. flos-aquae* (L.) Ralfs.)
	Stephanodiscus sp. Wf+		*Phormidium* Spr ff++ (*P. tenue* (Menegh.) Gom.)
	Fragillaria Wff+ (*F. capucina* Desmaz.)		*Lyngbia* Spr ff++ (*L. aerugineocoerulea* (Kutz.) Gom.)
		Schizomycetes	*Leptothrix* Spr ff+++ (*L. ochracea* Kutz.)
			Crenothrix Spr ff+ (*C. polyspora* Cohn.)
			Didymohelix sp. Spr f+
			Beggiatoa F fff+++ (*B. alba* (Vaucher) Trevisan)

gia, Monas, and *Codonella*) will be found from this figure to have played only a minor part in the seasonal variation of total plankton yield. Of the phytoplankton, diatoms were the most important component, attaining maxima and minima during winter and summer respectively. Chlorophyceae and Schizophyta represented significant components of the phytoplankton only during the winter pulses of 1945-46. The other components, *viz.*, Dinophyceae and Euglenineae were comparatively insignificant.

The frequencies of occurrence and relative abundances (during maxima) as components of respective family communities of the different phytoplankton genera are shown in Table I. *Geminella* will be found from this table to have been the major component of Chlorophyceae. The major components of Diatomaceae varied from year to year. Thus, for example, *Melosira* constituted the major component, being 54 per cent of the phytoplankton (3463 A.S.U./c.c. or 9 m.m.^{3}/lit. approximately) during the first week of January, 1946, while *Coscinodiscus* became the major component, being 100 per cent of the phytoplankton (1840 A.S.U./c.c. or 1 m.m.^{3}/lit. approximately) during last week of December, 1947. Similarly, *Nitzschia* and the "Remaining Diatoms" together became the major component in the 1946-47 winter. The two components, *Peridinium* and *Glenodinium* of the Dinophyceae were of equal magnitude. The major components of Euglenineae were *Euglena* and *Phacus*. The major components of Schizophyta were different during different parts of the year. Different species of *Oscillatoria* became the major components during fall and summer, the genus indicating a bimodal tendency of occurrence.

CORRELATIONS BETWEEN THE PHYSICAL AND CHEMICAL ENVIRONMENT AND THE YIELD AND PERIODICITY OF THE PLANKTON

The seasonal variations of the physical and chemical factors of the environment are shown in Fig. 2, curves G-Q. Comparing these with curves A-F, the following correlations will be found between the yield and periodicity of plankton and the physical and chemical environments.

Temperature.—Low winter temperature was associated with the Chlorophyceae pulses represented by *Geminella interrupta*. The Chlorophyceae pulses associated with the summer high temperature were almost entirely represented by Chlorococcales and Conjugales species. Winter low temperature was also associated with the largest yield of the diatom genera. But *Melosira* attained considerable yield during summer as well. *Navicula* also occurred during summer. *Coscinodiscus,* on the other hand, showed an inverse correlation of yield with temperature within 20° C to 31.5° C. No correlation, however, is apparent between temperature and *Synedra* and "Remaining Diatoms" yield. Any correlation is lacking between temperature and the yields of Schizophyta or of the different genera under this group separately. But the different temperature ranges of spring-summer and fall were associated with the

maxima of different *Oscillatoria* species, *viz.*, *O. agardhii* and *O. pseudogeminata*, respectively.

Rainfall.—Rainfall was inversely correlated with plankton yield. But this is not apparent during April to May, 1946.

Turbidity.—The highest and lowest turbidity ranges were associated with the minima and maxima of phytoplankton respectively. However, no correlation exists apparently between turbidity range and the holozoic protozoa yield.

Salinity.—The seasonal changes of salinity were inversely correlated with phytoplankton yield. But the yearly average of salinity increased every year, and had a direct correlation with corresponding increase of diatom-percentage in the annual average of total phytoplankton yield, though not with the absolute annual average yield of diatoms.

Alkalinity.—Alkalinity closely paralleled hardness due to bicarbonates, indicating the common constituents to be calcium and magnesium bicarbonates. The highest alkalinity was associated with the phytoplankton maxima, but no strict correlation is apparent between the weekly fluctuations of alkalinity and phyto-plankton yield.

pH.—pH was more or less stable within the range of 8.3 to 8.4.

Free-ammonia.—Free-ammonia N remained more or less constant, when fluctuations took place in the plankton yield. The relatively higher free-ammonia N concentration during some part of 1946 had also no apparent correlation with plankton yield.

Albuminoid-ammonia.—The lowest albuminoid-ammonia was associated with diatom or phytoplankton maxima.

Nitrite.—Nitrite N remained nil or trace, when considerable fluctuation occurred in phytoplankton yield. No correlation is also apparent between the exceptionally higher nitrite N figures and the phytoplankton yield and periodicity.

Nitrate.—The summer high and winter low nitrate N concentrations were associated with the minima and maxima of phytoplankton respectively. No definite correlation, however, is apparent between the weekly fluctuations of nitrate N concentration and phytoplankton yield.

Phosphate.—Phosphate concentration had varied within 0.001 to 0.0035 p.p.m. and shown the spring-summer highest and winter lowest in the past years. Assuming this to be normal for the years of this study also, the highest and lowest phosphate phosphorus would be associated with phytoplankton minimum and maximum, respectively.

Silicate.—Dissolved silica had varied within 5.25 to 22.2 p.p.m., reached a maximum during winter and more or less maintained this high value until late spring or early summer, in the past. With the consideration of the past records, the highest range of silica concentration would be associated with both maxima and minima of phytoplankton, mainly composed of diatoms.

Dissolved oxygen.—The highest dissolved oxygen concentration and saturation percentage were associated with the winter maxima of phytoplankton. The increase of these during November, 1945 and 1946, was simultaneous with the Schizophyta pulse-sequence. No correlation, however, is apparent between the weekly fluctuations of dissolved oxygen and phytoplankton yield. The highest dissolved oxygen concentration for the whole period of this study, attaining about 130.6 per cent saturation, was not associated with any corresponding increase of the phytoplankton yield.

Oxygen-consumption. — Lower oxygen-consumptions were associated with diatom or phytoplankton maxima.

Correlation between the Periodic Occurrence and Recurrence of the River Hooghly Phytoplankton and the Water-Filtration Troubles of Calcutta

The weekly average yield of diatoms and blue-green or green algae to a certain extent of the River Hooghly has some sort of a more or less direct correlation with the weekly average rate of chokage of the Calcutta filter beds during winter. Thus, the largest weekly yield of the River Hooghly diatoms during winter, 1945-46 was associated with the highest rate of filter chokage during the same period (*cf.* curves B and R, Fig. 2). Similarly, the smallest weekly yield of the diatoms was associated with the lowest rate of filter chokage during winter, 1946-47. This correlation is further confirmed by the presence of the same diatoms and other algae in sand or water of partly or fully choked filter beds during winter as occur in the River Hooghly during the same period. Moreover, the same diatoms or other organisms occurring in the river during winter constitute almost entirely the plankton of the settling-tank during the same period, the river water being drawn and stored in the settling-tank for filtration.

Discussion

The phytoplankton of the River Hooghly seem to be influenced principally by temperature and turbidity. Temperature appears to influence the time of occurrence of different phytoplankters, while turbidity appears to be inversely correlated with phytoplankton abundance. Thus, the diatoms appear to have some minimum, optimum, and maximum temperatures, *viz.*, below 20° C,

20°-23° C, and 31°-32° C respectively. Similarly, *Oscillatoria agardhii* and *O. pseudogeminata* occur within different ranges of temperatures, *viz.*, 24°-32° C, and 23°-29° C respectively. Again, the Chlorococcales and Conjugales genera on the one hand and *Geminella interrupta* on the other occur within different temperature ranges of 25° C-31° C and 20° C-21° C respectively.

It seems that the immense increase of current and turbidity, interfering with the photosynthetic metabolism of the organisms, prevents any significant phytoplankton yield during spring-summer, in spite of the abundance of chemical nutrients during this period. The turbidity is produced by the influx of the southwestern monsoon water, which seems also to dilute the phytoplankton yield. A similar correlation between turbidity and low basic productivity of the Missouri River with usually less common occurrence of phytoplankters than zooplankters was observed by Berner (1951), who held the high current velocity to be one of the principal factors promoting turbidity. Verduin (1951) attributed the twelve times greater spring diatom crop of Western Lake Erie in 1949 than in 1950 to the greater extent of turbid water in the Western basin during 1950. Butcher (1945-46), however, was of the opinion that current probably helps in the growth of the micro-algal flora of a river (He was referring to situations in which currents were not associated with turbidity).

Clearing of turbidity, on the other hand, results in an increased diatom or phytoplankton yield during winter. Nitrate- and albuminoid-nitrogen appear to be used up due to increase of photosynthesis, resulting in a lowering of their concentration. The role of phytoplankton was also advanced as explanation of the low nitrogenous matters of lakes, etc. by Beadle (1932-34), Harold (1934), and Hutchinson *et al.* (1932), and of the low nitrite and nitrate content of the tropical seas by Atkin (1932-33). Phosphate phosphorus also seems to be lowered during this period by way of algal consumption. The utilization of soluble organic matter by diatoms, as is indicated by lowering of albuminoid nitrogen, also results in lowering oxygen-consumption. The preference for slightly contaminated water or utilization of organic substances by diatoms was also stated by West, W. (1911-12), Hutchinson (1944), Harvey (1945), Pearsall *et al.* (1946) and others. A direct relation between albuminoid nitrogen and soluble organic matter was regularly advocated by Drew (1914).

The steady rise of the annual average of salinity, every year, associated with increasing percentages of diatoms in the annual averages of phytoplankton abundance seems to indicate a direct relationship between salinity and the diatoms, while the apparently inverse relationship between their seasonal variations may be explained as due to the turbidity interference on the growth of the latter. This seems, likely as one of the probabilities, because of the river water approaching seawater characteristics, owing to the absence of any fresh water flow except in the rainy season, and the gradual reduction of its capacity to hold the monsoon water due to a gradual raising of its bed-level.

The increase of dissolved-oxygen in winter and sometimes in late fall does not seem to be simply due to the falling temperatures but seems to be induced by the phytoplankton growth during these periods. The high dissolved-oxygen during spring-summer, when there is relatively much higher dissolved organic matter and much smaller phytoplankton yield, however, cannot be explained but for greater turbulence by wave action resulting in higher diffusion and absorption of oxygen and promotion of oxygen dissemination, and surface evaporation resulting in greater streaming effects in the downward direction.

Summary

The ecology of the River Hooghly was studied with reference to the micro-algal effects produced in the water supplies of Calcutta. The phytoplankton played the major part and are considered in detail. The best represented class were Diatomaceae which also occurred both as seasonal and annual dominants. Most favourable growth of the diatoms took place during winter, while only restricted growth of *Nitzschia* (*N. linearis, N. acicularis*) and *Synedra* (*S. ulna, S. pulchella, S. affinis*) occurred during spring-summer. Chlorophyceae also showed maxima during winter, when they were solely represented by *Geminella interrupta*. Chlorococcales and Conjugales genera were found only during the least significant spring-summer pulses. The fall pulse of the phytoplankton was mainly due to *Oscillatoria pseudogeminata*, while a summer pulse of *Oscillatoria agardhii* appeared.

The yields of the phytoplankton were inversely correlated with turbidity and rainfall. Alkalinity, principally due to calcium and magnesium bicarbonates, reached the maximum when the largest yield was attained by the phytoplankton.

The nitrate- and albuminoid-N concentrations and seemingly the phosphate-P concentration were inversely related to phytoplankton yield. But the soluble silica seemingly maintained almost equal concentrations both during the largest- and smallest-diatom-yielding periods.

The highest oxygen saturation percentage and lowest oxygen consumption (permanganate) were generally attained during the largest phytoplankton yield.

The annual averages of salinity as well as the percentage yield of diatoms indicated a rising tendency over the three-year period of this study.

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THE LIFE HISTORY OF THE SPINY-TAILED FAIRY SHRIMP IN LOUISIANA

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The "spiny-tailed fairy shrimp," as Creaser (1930) referred to *Streptocephalus seali* Ryder, has been recorded from seventeen states in all sections of the United States, as well as from Canada and Mexico. Although it is probably the most widely distributed of all the North American fairy shrimps, it remains one of the least known. Extensive ecological and life history studies have been carried out by several investigators on various species of other genera. Probably these widely known studies are the source of the frequently encountered statements to the effect that fairy shrimp are cool water dwellers, appearing in temporary pools only during the early spring months and then disappearing until the following spring. Such statements, while generally true of many species of fairy shrimps, especially of the *genus Eubranchipus,* have no validity for the North American streptocephalids.

In an earlier publication (Moore 1951) the writer presented observations on the the biology of *S. seali* based on eight months' field and laboratory studies. At the present writing several of the field stations have been under regular and frequent observation for over two years. Certain earlier conclusions may now be supplemented by additional data, and observations on the seasonal activities and growth rates of the species throughout the entire annual cycle are now available.

METHODS

Collections were made with dip nets of fine mesh brussels netting; newly hatched larvae and early instars were collected with dip nets of silk bolting cloth. Specimens were preserved in the field in 10% formalin. Measurements were made under a binocular microscope, from the front of the head to the tip of the cercopods but not including the terminal setae.

Water temperatures were taken with a standard laboratory thermometer, the instrument being shaded while the determination was made. Water samples for field and laboratory analysis could not be collected with the customary limnological sampling devices due to the very shallow nature of many of the habitats. An Irwin Sampler (Welch 1948, pp. 204-206) was constructed and used for this purpose. Chemical methods employed were the standard procedures recommended by the American Public Health Association (1946). Turbidity was determined with the Jackson turbidimeter, and hydrogen ion concentrations were checked with a Hellige pocket comparator and a Beckman pH meter.

DISTRIBUTION AND GENERAL NOTES

Extensive dip-netting of pools and ditches has been carried on in nearly every section of Louisiana. In addition to the localities previously reported (Moore 1951), *S. seali* has been collected by the author from ditches near Reeves, Allen Parish, and by H. B. Chase from the vicinity of Greensburg, St. Helena Parish. Behre (1950) has reported the species from rain water pools on Grand Isle, Jefferson Parish.

The fairy shrimps, while sometimes locally abundant, have a very spotty distribution over the state. They appear to be most abundant in seasonal pools and ditches in the acid, sandy soils of the pine hills of the western and central portions of the state; and in similar habitats in the pine barrens of the Florida Parishes (*i.e.* the portion of the state north and east of the Mississippi River). They are almost entirely absent from pools in the muck soils of the coastal marshes and the Mississippi River alluvial plain. In the last-named localities the water table is high and pools and ditches rarely dry out completely. Small fishes (especially *Gambusia affinis*), amphibians, and predatory invertebrates probably prevent the establishment of anostracan populations in these pools. The two recorded occurrences of *S. seali* in these areas were in rather special habitats. One was a newly dug borrow pit in which the shrimps did not occur after the first season; the other was in rain pools on the Grand Isle beaches bordering the Gulf of Mexico.

While the agents of dispersal of fairy shrimps to new localities are still largely a matter of conjecture there can be no doubt that among them might be listed those agencies (semi-aquatic animals, wind, human) which could transfer the dried, egg-containing silt from a populated habitat to an unpopulated basin. The successful introduction of *Eubranchipus vernalis* (Verrill) to a new pool through transference of mature adults has been described by Dexter and Kuehnle (1948). The present author has similarly succeeded in introducing *S. seali* into a seasonal pond not previously containing the animal. The basin, a water

oak-mayhaw pond in the pine woods west of Alton, St. Tammany Parish, was first observed on November 15, 1950. During the ensuing eighteen months, through several cycles of alternate flooding and drying, repeated careful checking of the pond failed to reveal any trace of the anostracans. On June 3, 1952 about a dozen mature *S. seali,* including egg-bearing females, were transferred to the pool from a ditch habitat. The forest pool soon afterward dried out and remained dry until December 30 when a three-and-one-half-inch rainfall within the space of a few hours flooded the basin to a depth of two feet. The pool was not visited again until February 16, 1953 on which occasion moderate numbers of adult *S. seali* of both sexes were collected. It is perhaps noteworthy that all specimens taken were dark brown in color, tinged with deep green—typical coloration of forest pool shrimps. The specimens which had been used to "inoculate" the pool were the ditch forms, completely unpigmented except for black eyes and orange-red cercopods.

Physico-Chemical Factors

In a previous publication (Moore 1951) the physico-chemical factors of *S. seali* habitats in Louisiana were characterized as showing wide extremes of temperature and turbidity, low hydrogen-ion concentrations (pH 5.2-6.1), and very low total alkalinities (4.0-10.5 ppm). Continued observation of these habitats and of others subsequently discovered permits modification and amplification of certain of these values.

The lowest hydrogen-ion concentration recorded was pH 4.9 for a peat-bottomed forest pool near Florenville, St. Tammany Parish. The highest was pH 6.2 for a ditch habitat in Grant Parish. This ditch also had a total alkalinity of 15.0 ppm, which is very low, but the maximum recorded for a Louisiana habitat. A temporary rain pool habitat on the beach near Waveland, Hancock County, Mississippi tested 134.5 ppm total alkalinity. This pool, which also received brackish water by way of seepage and wave spray from nearby Mississippi Sound, tested 315.0 ppm of chloride. It furnishes an interesting instance of the toleration of mildly brackish conditions by a fresh-water branchiopod.

Water color was consistently high in the forest pools, the maximum recorded being 360; values of 200-225 were common. Ditch habitats showed much lower water color indices. Turbidities varied in the opposite fashion, the waters of the forest pools were clear with turbidities consistently less than 25 ppm, while the ditch habitats characteristically showed turbidities of 80-550 ppm, with a maximum of 3000 ppm being recorded from a ditch pond in Tangipahoa Parish.

Free carbon dioxide and dissolved oxygen determinations were made only on a few occasions and then only at certain of the forest pool habitats. Decomposing leaves and other plant debris on the bottoms of these pools was probably reponsible for the relatively high free carbon dioxide (17.0-20.0 ppm) and for oxygen tensions (1.0-4.5 ppm) of less than saturation levels.

Water temperatures showed a tremendous range. The minimum temperature recorded by the author was 8.0° C. for a ditch pond on November 22, 1952. Mr. Henry Chase (personal communication) reports collecting *S. seali* in St. Helena Parish in January, 1940 when the air temperature was minus 3° C. and a film of ice covered the surface of the shallow pond.

At the other extreme, the writer has collected *S. seali* from shallow ditches exposed to full sun with water temperatures of 35° C. or higher on no less than eleven separate occasions during the midsummer months (June-August) of 1951-52. The maximum temperature recorded was 42° C. on June 27, 1951. The habitat involved was a roadside ditch, nearly dry, with a maximum depth of only three inches. Air temperature was 35° C. (shade), but the ditch was not in the least shaded. A few tadpoles and a dragon fly naiad were collected along with a considerable number of mature *S. seali,* in apparently good condition despite the extremely high temperature. In this connection it might be mentioned that a related species, *Streptocephalus texanus* Packard, has been recorded (Moore 1950) at a water temperature of 36.4°C. *Eubranchipus vernalis* has been reported by Dexter and Kuehnle (1951) at a temperature of 25° C., unusually high for this species which does not ordinarily tolerate temperatures of over 21° C. (Dexter 1946).

Periods of Occurrence

The times of occurrence of *S. seali* at three stations during the period August 1950 to March 1952 are indicated on Figure 1. Stations 1 and 3 are shallow ditches bordering a gravel road approximately 1.6 miles west of Alton, St. Tammany Parish, Louisiana. Excessively heavy rainfall occasionally flooded these ditches to a depth of two feet and resulted in an inflow of water from nearby semi-permanent streams in the bordering pine woods. At such times the small fish (chiefly *Gambusia*) brought in with the floodwaters quickly eliminated any fairy shrimp present; no more would be seen until a period of drying had destroyed the predators, and sub-

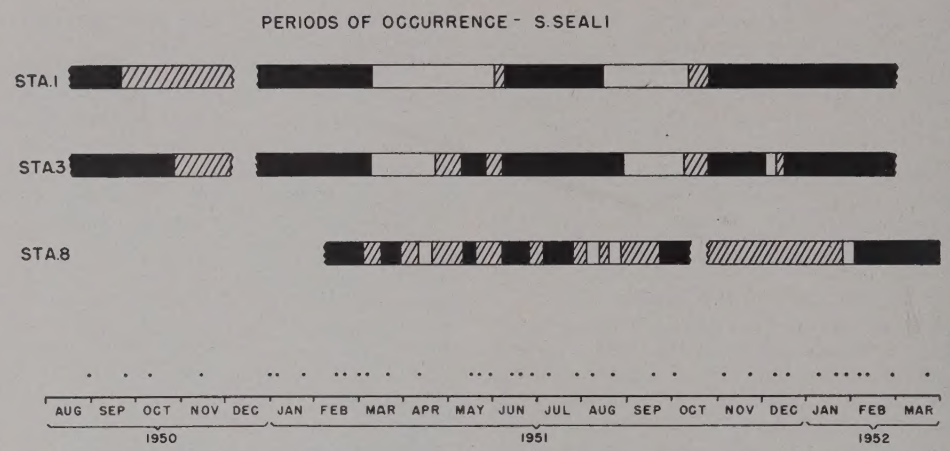

FIG. 1. Periods of occurrence of *Streptocephalus seali* in three typical habitats. Black bar indicates fairy shrimp present; white bar, habitat flooded but no shrimp present; shaded bar, habitat dry. Dots show times of field visits.

sequent flooding once more prepared the habitat for a new generation of the anostracans.

Station 8 is a water oak-sour gum pond in the pine woods near Alton. This basin not only received natural drainage from the surrounding area, but was close to a gravel road and collected the runoff from the bordering roadside ditch. Thus a relatively small amount of precipitation would result in a considerable accumulation of water in the basin. However, this pond was short-lived, during the summer months particularly, and rarely remained filled for longer than two or three weeks at a time.

In the ditches (Stations 1 and 3) there appeared to be two main periods of flooding of the habitats during the year, separated by dry periods of varying duration. Each period of flooding was accompanied by the development of a large population of the anostracans. Both the winter and the summer populations in 1951 were eliminated, in March and August respectively, by heavy rains which overflowed the ditches and brought in numerous small fishes from nearby streams. The unusually long life span (over 16 weeks) at Station 1, from late October 1951 through March 1952, is attributed to a lesser amount of flooding in December which resulted in a second hatching of eggs from the previously dried out borders and ends of the ditches. In other words, after December 1951 two broods of *S. seali* were present together and, as the second brood matured, they became indistinguishable from the survivors of the first hatch.

Station 3 was the shallower of the two ditch habitats, consequently it dried out more rapidly. In such a condition a heavy rain would result in a moderate accumulation of water in the ditch and, if it persisted for a few days, a population of the anostracans would develop. Thus there were four successive populations of *S. seali* at Station 3 during the period May 1951 through February 1952. The first of these survived for less than two weeks and failed to reach maturity due to drying of the ditch. The other three populations probably represent distinct and separate generations, however, since fully mature specimens of both sexes were present in each case.

The piney-woods pool (Station 8), subject as it was to frequent drying and refilling, exhibited a striking sequence of fairy shrimp populations. During the one-year period, from February 1951 to February 1952, there were recorded no less than seven successive occurrences of *S. seali*, separated by periods of drying of the pool. Not all broods reached maturity; however mature males and ovigerous females were taken in four of these populations: on March 3, June 20, and October 2, 1951, and on February 29, 1952. The occurrence of several distinct generations per year of *S. seali* in the natural habitat thus is strongly indicated, although it would be virtually impossible to prove that the successive generations did not originate from repeated hatchings of a single earlier deposition of eggs.

Two generations of *S. seali* during a single summer season have previously been noted by Packard (1883); and of *Streptocephalus texanus* by Moore (1950). Two broods of *Branchinecta lindahli*

Packard[1] in a pool which dried in the interim have also been recorded (Moore, 1950), although in this instance it is probable that two distinct generations were not involved. Two or three broods of *Eubranchipus vernalis* have been reported by Dexter (1946) and Dexter and Kuehnle (1948); although in only one instance was there an intermediate period of drying and the investigators attributed multiple broods in each case to successive hatchings from an earlier deposition of eggs.

It would appear that the periodic incidence of *S. seali* in Louisiana may thus be correlated with the factors of precipitation and evaporation, rather than with a factor such as temperature which is critical for certain species of the genus *Eubranchipus*. As often as a suitable habitat dries and refills, just so often will populations of *S. seali* appear. The flooded conditions, of course, must persist for at least several days, and the presence of predators (*i.e.*, fishes) will prevent the development of the anostracan population. Temperature, however, does not exercise any controlling influence in the locality under consideration.

Life Cycle

Incubation period

It is very difficult to determine the interval between filling of a pool and hatching of the eggs unless daily visits are made. The distance of the present habitats from New Orleans (50 miles) made such frequent visits impossible. However on two occasions when young larvae were collected by fine-meshed plankton net at Station 8, the time of filling of the pool is known with a high degree of certainty and the minimum hatching period may thus be estimated.

On January 21, 1952 the pond was observed to be perfectly dry. No significant precipitation occurred until the early morning hours of January 28, when over two inches of rain fell within a space of five hours. On January 30, approximately sixty hours after commencement of this rain, the pond was visited and observed to be filled to a depth of one foot with turbid, muddy water. Air temperature at this time was 9.5° C.; water temperature was 11° C. A plankton collection contained larval copepods, small Cladocera, mosquito larvae, and numerous metanauplei and early larval instars of the fairy shrimp.

Again, on December 20, 1952 the basin was visited and observed to be dry. Intermittent rainfall occurred during the next few days but probably not in sufficient quantity to result in any accumulation of water in the basin. A three and one-half inch rainfall took place during the morning hours of December 30, and on December 31 the pool, probably about thirty hours old, was visited. It was filled to a depth of two feet with turbid water. Air temperature was 16° C.; water temperature was 12° C. A plankton sample contained larval copepods, small Cladocera, mosquito larvae, small isopods, and a very few anostraca metanauplei.

One may conclude that hatching of the dried eggs of *S. seali* begins within thirty hours after immersion. It probably continues for several hours or days thereafter. Under circumstances in which a pool fills in several stages, inundating additional areas of dried-out border with each rise in water level, there will occur, of course, several successively hatched broods of the fairy shrimp in the same pool.

Winter growth rate

In order to accurately determine the growth rate of a short-lived animal such as *S. seali* one should have measurements of an adequate sample of the population made at frequent intervals during the life span—that is, collections should be made at daily intervals during the initial stages of the cycle, and at weekly intervals after sexual maturity has been attained. Since all habitats known to the writer were far distant, such frequent observations were manifestly impracticable. Further, discovery of several populations was made only after the intitial stages of development had been completed; in other cases the systematic study of a population had to be terminated prematurely due to drying of the pool or, occasionally, to flooding which brought in predators from nearby permanent bodies of water. However a number of complete or nearly complete life cycles have been studied and, since *S. seali* is known to occur during every month of the year in Louisiana, curves have been prepared illustrating growth rates for both the summer and winter seasons. Only situations where field observations and length distribution curves indicated a single major brood to be present are considered in the following discussion.

A winter growth curve, based on collections made at ditch Station 1 during the period November 12, 1952 through February 28, 1953, is shown in Figure 2. Increase in length, it will be noted, took place at a variable rate although some growth continued throughout the entire life span. The females, with one minor exception, were con-

[1] This species was identified in the reference cited as *B. coloradensis* Packard. In the light of Mackin's (1952) reexamination of the nomenclature of the genus it has been established that the writer was actually dealing with *B. lindahli*. Dr. Mackin has seen and verified the writer's corrected identification.

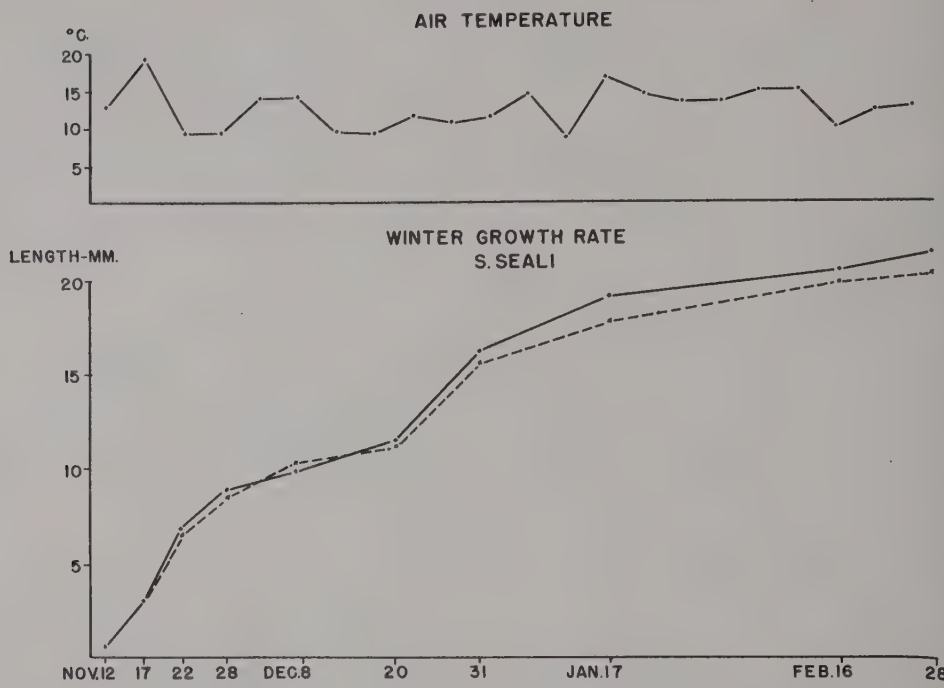

FIG. 2. Upper graph: general temperature trends based on five-day averages of daily mean temperatures. Lower graph: winter growth of *Streptocephalus seali*. Solid line, males; broken line, females.

sistently slightly smaller than the males in a given population. Sexing of the individuals comprising the first two collections was not attempted since sex distinctions are uncertain in small specimens.

From November 12, at which time the recently flooded ditch supported a large population of metanauplei and early larval stages averaging 0.57 mm. in length, until November 28, the growth rate was rapid. It averaged 0.51 mm. per day and during one five-day period (November 17-22) was as high as 0.70 mm. per day. At the end of this rapid growth phase the mean length for both sexes combined was 8.8 mm. The larger females (10-11 mm.) had well developed egg sacs at this time, but none carried eggs; a few of the larger (11 mm.) males possessed essentially adult (spine-tipped) cercopods and scissor-like claspers, but the vast majority of both sexes were still juvenile.

During the ensuing three week period (until December 20) growth was much slower, averaging only 0.12 mm. per day. About 15% of the females taken during this period were observed to be carrying eggs, from two or three to a maximum of twenty per individual. These ovigerous females were all 12 to 13 mm. in length, somewhat longer than the average.

A second period of accelerated growth took place between December 20 and 31, during which time increase in length occurred at the rate of 0.41 mm. per day. The growth rate then gradually declined until toward the end of the life cycle it was only 0.05 mm. per day. Only a small proportion of the females taken during late December carried eggs and those which did bore only a few. By mid-January, when the mean length of the females had reached 18 mm. the majority had well-filled ovisacs containing from 75 to 175 mature eggs.

Water temperatures were determined at the time of each collection and were found to range between 11.5 and 21.0° C. Since these determinations were made at too infrequent and irregular intervals to give a true picture of temperature trends, and since the shallowness and exposed nature of the ditch habitat would imply a close correlation between air and water temperatures, mean daily air temperatures were calculated from the tabulations of the U.S. Weather Bureau (Covington Station) for the period under consideration. Daily temperature means proved to be so variable that general temperature trends were obscured, hence the daily mean temperatures were averaged

for five-day intervals and the averages plotted to give a "smoother" curve.

It will be noted that there is little positive correlation between growth rate and mean air temperatures. In fact, the period of most rapid growth is a period of declining temperatures, while the subsequent period of growth retardation is associated with both rising and falling temperatures. The implication is clear that some factor or factors other than temperature is responsible for the variations in the growth rate of *S. seali.*

Growth rate studies by Coopey (1950) and Dexter and Kuehnle (1951) on certain species of the genus *Eubranchipus* have shown a growth pattern, similar in many respects to that here recorded for *S. seali.* These investigators reported an initial period of rapid growth, an intermediate period of marked growth retardation, and a later period when the growth rate approached but did not attain the rate of the initial phase. The onset of the period of retarded growth was shown to be independent of any temperature drop, although it was suggested that its duration might be dependent upon water temperatures and available food. These investigators associated the slowing of the growth rate with the maturing of the gonads. Coopey noted that in *E. oregonus* the retardation was more marked in females, although it was noticeable in males as well.

In the case of *S. seali* it would appear that egg production during the winter season commences on a very limited scale during the period of growth retardation. The subsequent resumption of rapid growth is associated with a corresponding decline in the rate of egg production. As the growth rate gradually subsides once more, the development of mature ova resumes at a greatly accelerated rate. Perhaps a more nearly correct interpretation of the data is that suggested by Coopey (*op. cit.*), that "some influence associated with the maturing of the sex products retards the growth rate."

Summer growth rate

Figure 3 illustrates the growth rate of *S. seali* during the summer season. The population, at ditch Station 1, was first observed on June 13, 1951. The ditch at this time was recently flooded; two weeks previously it had been dry. Fairy shrimp were collected regularly until July 26; on August 8 only a very few large individuals were seen and no collections were made. On August 22 repeated dipping failed to reveal any shrimp. The population, therefore, had persisted for about two months. Although moderate numbers of predatory invertebrates (Coleoptera larvae, Odonata naiads, Hemiptera nymphs) were observed on the latter dates it is not thought that they were present in sufficient numbers to be more than a minor factor in the elimination of the fairy shrimp population. It seems more probable that the anostracans had completed their life cycle by early August and were gradually dying off.

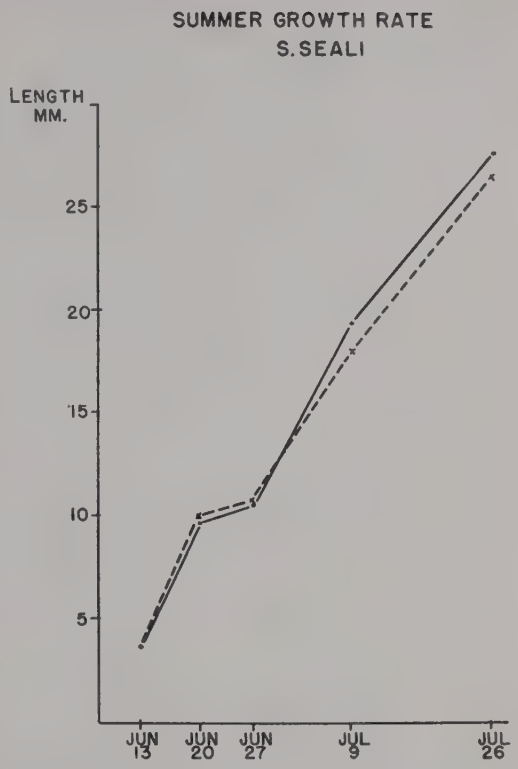

FIG. 3. Summer growth of *Streptocephalus seali.* Solid line, males; broken line, females.

Water temperatures recorded at the time of each collection ranged between 31 and 39° C. Since the Covington Weather Station does not operate during July and August, and since there are no other nearby Weather Stations to provide comparable data, it is not possible to provide a record of the mean air temperatures for this period.

Note that the growth phases previously described are expressed on the curves illustrated in Figure 3. As with the winter brood, the females of a given population tended to run slightly smaller than the males. Individuals collected on June 13 ranged from 2.6 to 4.8 mm. in length, with a mean length of 3.6 mm. Sex distinction at this time was uncertain; consequently no separation has been attempted on this basis. Rapid growth at the rate of 0.9 mm. per day occurred between June 13 and June 20. This was followed by a seven-day period of marked growth retardation,

with an average increase in length of only 0.1 mm. per day. It is possible that the growth retardation phase was actually somewhat longer than is indicated on the graph; since the subsequent collection was not made until twelve days had elapsed it is impossible to state with certainty just when the second accelerated growth phase commenced. Rapid growth, averaging 0.58 mm. per day, then continued for as long as the population was available. There was no apparent flattening of the growth curve toward the end of the life cycle as was found in the winter population, although collections were probably not made with sufficient frequency to demonstrate such flattening if it did occur. Collections made on August 8 contained only a very few large male individuals which were not preserved; this record therefore does not appear on the graph.

Specimens collected during the growth retardation phase, from June 20 through June 27, were subjected to special study. During this period both sexes attained a considerable degree of development of the adult sex characters. The larger females had ovisacs up to 2.5 mm. in length containing a small number (2 to 12) mature ova; the smaller females had shorter ovisacs (1.6 to 2.0 mm.) with numerous small eggs in the ducts. The larger males were essentially mature with fully developed claspers, spine-tipped cercopods, and well-filled sperm ducts. Smaller males still retained certain juvenile characters including pincer-like claspers, setiferous cercopods without spiny tips, and had no evidence of sperm in the ducts. The majority of the individuals of both sexes, although still small in size, showed definite evidence of at least incipient sexual maturity.

During the subsequent rapid growth phase from June 27 through July 26 egg production was enormously increased, especially towards the end. Specimens taken on July 9 had up to 75 mature ova in the ovisacs, with evidence of further active proliferation from the ovaries. On July 26 over 450 mature ova were counted from the ovisac of a single female, with many more still to be released from the swollen ovaries. Egg production evidently occurs at a much greater rate during summer than winter, probably due to the more abundant food supply and more favorable temperature conditions.

The maximum rate of growth and the shortest complete life cycle recorded for *S. seali* was observed at forest pool Station 8 during this same period. The basin, dry on May 30, 1951, was found to be newly flooded on June 13. The only significant precipitation in the area had occurred on June 11, hence the pool was probably about 48 hours old at the time of the initial visit. Plankton net collections revealed a large population of tiny fairy shrimp averaging only 2.0 mm. in length. One week later, on June 20, the mean length had increased to 16.0 mm. The males, averaging 16.9 mm., were mostly fully mature. The females (mean length: 15.2 mm.) were in the initial stages of egg production, carrying from one to twenty mature ova. Seven days later, on June 27, the pool had dried completely.

The entire period during which the pool was in existence, and the maximum possible life span of the anostracans, was probably no longer than sixteen days. The interval from flooding of the basin to the attainment of sexual maturity was no more than nine days. Growth rate of the shrimp was approximately 2 mm. per day for the period between the two collections. As might be expected, temperatures were high. Water temperatures recorded on June 13 and 20 were 27.5 and 28.0° C., respectively. Mean daily air temperatures (U.S. Weather Bureau records) ranged from 24 to 27° C., with daily maxima of 30 to 34° C.

Increase in length of 2 to 2.5 mm. per day was recorded by the writer (1950) for *S. texanus*. In this instance the duration of the life cycle was not observed. Dexter (*op. cit.*) reported a case of unusually rapid growth in *E. vernalis* in which egg development was noted within two weeks after hatching, and the population completed its entire existence in about 32 days. Measurements given for one seven day period indicate a growth rate of 1.24 mm. per day.

Sex ratio

Few published references to sex ratios in the anostraca are available. Weaver (1943) reported a 5:1 preponderance of females in *E. vernalis* early in the season, a subsequent increase in the proportion of males, and finally a decrease in the relative number of males late in the season. Dexter (*op. cit.*), with reference to the same species, noted a general preponderance of females (an over-all ratio of 1 male to 1.5 females) in collections made at various localities and at various times during the spring months. He did not observe any change in sex ratio during the season. In a subsequent study, Dexter and Kuehnle (1951) reported a consistent preponderance of males over females in certain areas of northeastern Ohio, while females predominated in other areas. Coopey (*op. cit.*), in studies on *E. oregonus*, reported a fairly even sex ratio early in the cycle with a definite and marked decline in the number of males as the season progressed.

He observed that the mature females persisted in the ponds for eight to eleven weeks after all males had died off.

With respect to *S. seali,* random samples were drawn from the winter and summer populations previously described and checked as to sex. The results of these counts are given in Table I. The object was not only to determine the sex ratio at a given time but also to check possible changes as the population aged. The earlier collections of each series in which the mean body length was less than 4 mm. were not included in this study due to the uncertainty of sex distinction of these small individuals.

TABLE I. *Sex ratios,* Streptocephalus seali.

Winter population			Summer population		
Date	No. sexed	Ratio males: females	Date	No. sexed	Ratio males: females
XI-22-'52...	125	1:1.23	VI-20-'51...	157	1:1.00
XI-28-'52...	94	1:1.35	VI-27-'51...	157	1:1.10
XII- 8-'52...	154	1:1.37	VII- 9-'51...	58	1:1.00
XII-20-'52...	147	1:1.37	VII-26-'51...	9	1:0.50
XII-31-'52...	171	1:1.38			
I-17-'53...	261	1:1.23			
II-16-'53...	53	1:1.50			
II-28-'53...	65	1:0.90			

The winter population showed a definite preponderance of females throughout the entire cycle except on the last collection date when a slight excess of males was taken. The sex ratios for the entire series showed an average of 1.28 females to each male. Only the last two collections varied markedly from the mean and even this departure may be more apparent than real. As the aging population declined in numbers the individuals were more dispersed throughout the habitat and it became increasingly difficult to collect a sufficiently large sample to be truly representative.

The summer brood showed a nearly constant 1:1 ratio between the sexes until the last collection date when males outnumbered females two to one. As in the previous instance, this apparently marked change in sex ratio may in part be due to the smallness of the final collection.

The author does not believe that the male-female sex ratios of 1:1.28 for winter populations, and 1:1 for summer populations represent a constant difference based on seasonal factors. Spot checks of many isolated collections made during the winter months frequently showed a nearly 1:1 ratio; occasionally males were even more abundant than females. It does seem a safe generalization from the data at hand, however, to state that young populations of *S. seali* usually show a uniform sex ratio, or a slight preponderance of females over males. No significant changes in this ratio occur, at least until the population is very old and all individuals have long since attained sexual maturity. There does seem to be a tendency for the last survivors of a brood to be predominantly of one sex but it is as often apt to be males which survive as females. There is no indication in *S. seali* of anything like the prolonged survival of mature females after the death of the entire male population, as Coopey reported for *E. oregonus.*

Summary of the life cycle

Hatching of the dried eggs of *S. seali* commences soon after inundation of the habitat. During the winter months hatching will begin within thirty hours. In summer, larvae averaging 2.0 mm. in length have been collected forty-eight hours after flooding of the pool indicating that hatching is probably even more rapid at elevated temperatures.

The early stages of growth are passed quickly. Increase in length of 0.5 mm. per day (winter) and 0.9 mm. per day (summer) have been recorded in typical instances, with maximal rates of 0.7 and 2.0 mm. per day respectively. Usually within one to three weeks, depending upon the season, the members of the brood have attained a length of 10 to 12 mm. and show definite evidence of incipient sexual maturity.

There follows an interval of one to three weeks duration of very marked growth retardation. Increase in size during this period is surprisingly uniform (*ca.* 0.1 mm. per day) at both summer and winter temperatures. Individuals of both sexes develop adult characters and, in the case of the females, the production of mature ova on a very limited scale occurs toward the close of this phase.

A second period of accelerated growth then takes place. In typical summer broods the growth rate may approximate 0.6 mm. per day and may continue for perhaps four or five weeks or even longer unless some accident causes the death of the population. Egg production occurs at an increasingly rapid rate during this entire period.

A similar period of accelerated growth follows the retardation phase in the winter broods. In this case, however, the growth rate is somewhat less (0.4-0.5 mm. per day) and it further declines toward the end of the life span. Unlike the summer brood, egg production is at a virtual standstill during the initial stages of this rapid growth phase although it resumes again later in the cycle when the growth rate has begun to decrease.

Summary

1. The distribution of *Streptocephalus seali* in Louisiana, based on intensive collecting activity over a period of several years, is outlined. The introduction of the species through transference of mature adults into a seasonal pool not previously known to harbor it is described.

2. Louisiana habitats all showed low hydrogen ion concentrations (pH 4.9-6.2), low total alkalinities (4.0-15.0 ppm), and wide extremes of color (maximum: 360) and turbidity (maximum: 3000 ppm). A beach pool habitat on the Mississippi Gulf coast showed a total alkalinity of 134.5 ppm, and a chloride content of 315 ppm.

3. *S. seali* has been collected in Louisiana during every month of the year. Several successive generations during the year have been observed in pools subject to alternate flooding and drying —the maximum number of separate occurrences during any twelve month period being seven.

4. The species has been observed to occur at an extremely wide range of temperatures—from near-freezing temperatures in an ice-covered pool, to a maximum temperature of 42° C.

5. Hatching of the eggs commences within thirty hours following flooding of the habitat. Growth is characterized by an initial period of very rapid increase in length, an intermediate period of marked growth retardation, and a final phase during which rapid growth is resumed. Typical growth rates for both winter and summer broods are presented.

6. Egg production on a limited scale commences during the middle period of retarded growth. In the shorter-lived, more rapidly growing summer broods it continues uninterruptedly and at an increasing rate throughout the subsequent life span. Winter populations show in apparent cessation of egg production in the early stages of the third growth phase, with an active resumption of egg production later in the life cycle.

7. The maximum growth rate (2.0 mm. per day) and the shortest complete life cycle (16 days from flooding of the pool until drying) was observed in a forest pool habitat during June, 1951.

8. The ratio of males to females in natural populations of *S. seali* is approximately 1 : 1, and shows no consistent change during the life cycle.

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POLLEN PROFILES FROM PRINCE WILLIAM SOUND AND SOUTHEASTERN KENAI PENINSULA, ALASKA

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Two earlier papers discussed the pollen and peat stratigraphy of southeastern Alaska muskegs and its relation to postglacial phytogeography, climate, glacier variation, land-sea level fluctuation, and vulcanism (Heusser 1952, 1954). In an effort to extend these studies to the northwest along the border of the Gulf of Alaska, five peat sections were taken from muskegs in coastal southern Alaska, on southeastern Kenai Peninsula, and on eastern Prince William Sound. The localities at which muskegs have been sampled are shown by number on the accompanying sketch map (Fig. 1).

One of the objectives of this paper is to trace the postglacial dispersal of the trees of the Coast Forest Formation in this district. Furthermore, since the district is at present part of an ecotone or transition between tundra and the coast forest (Cooper 1942), another objective is to show the postglacial relation of these two formations. The study region is also of interest in that it represents the northern terminus for two members of the coast forest. Western hemlock (*Tsuga heterophylla*[1]), which comprises almost 75 per cent of this forest in the Alexander Archipelago (Taylor 1932), 500 to 800 miles southeastward, and Alaska yellow cedar (*Chamaecyparis nootkatensis*) extend as far as western Prince William Sound.

Recent palynological investigations by Livingstone (1953), Hansen (1953), and the Alaska Terrain and Permafrost Section of the U. S. Geological Survey (William S. Benninghoff, personal communication) and those made earlier by Bowman (1934) and Knox (Judson 1946) are gradually unfolding the postglacial and earlier Pleistocene events in the Territory. Geologists, in addition, are making a concerted effort to map the Pleistocene glaciations and construct a chronology (Péwé, *et al.* 1953). It is the purpose of this paper to add to this evolving store of information and at the same time to augment our knowledge of the postglacial development of the Coast Forest Formation as we know it today.

Field work connected with this study was supported by a Sigma Xi-Resa Grant-in-Aid and a grant from the Glacier Study Project of the American Geographical Society. Travel to the Territory was afforded by the Juneau Ice Field Research Project which is administered by the

[1] Nomenclature follows Hultén (1941-1950); in some cases plant names given in references cited in the text have been changed to follow Hultén.

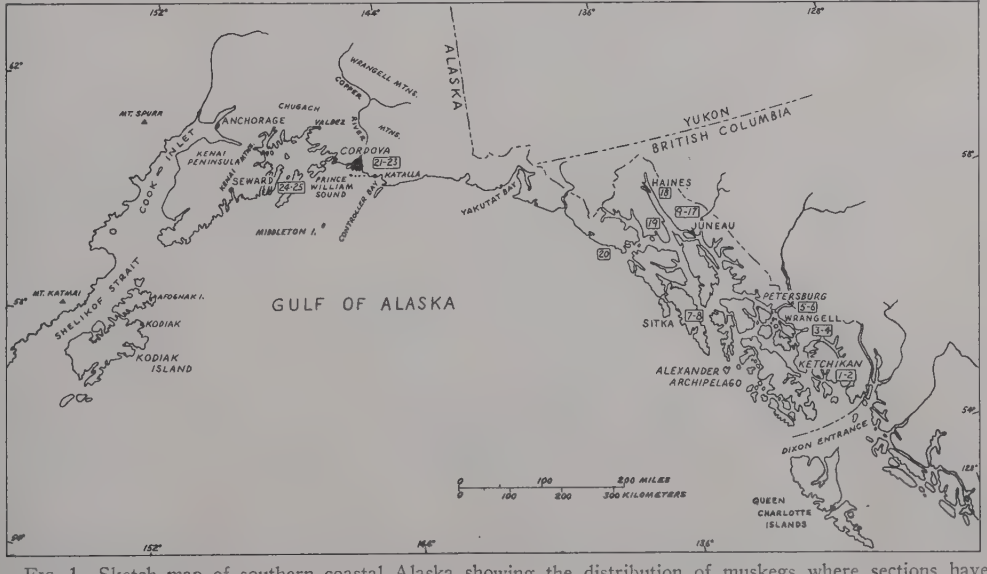

FIG. 1. Sketch map of southern coastal Alaska showing the distribution of muskegs where sections have been taken for this study and those earlier.

Society under contract with the Office of Naval Research. The preparation of the peat and the microscopic study were carried out in the Osborn Memorial Laboratories at Yale University with the aid of the Theresa Seessel Fellowship. To these organizations and the following, especial thanks are recorded: William O. Field of the American Geographical Society, B. Frank Heintzleman, Governor of Alaska, William S. Benninghoff and Thor N. V. Karlstrom of the U. S. Geological Survey, and the U. S. Forest Service personnel: Alva W. Blackerby of the Tongass National Forest in Juneau, Clyde Maycock in Cordova, and R. A. Schwartz and his assistant, Tom Seiger, in Seward, these last of the Chugach National Forest.

Physiography

The northern part of the Gulf of Alaska penetrates the coast in two large embayments separated by the Kenai Peninsula (Fig. 1). Cook Inlet is to the northwest of the peninsula; Prince William Sound with its archipelago is just eastward, and Copper River Delta is to the east of the sound. The sound is approximately 80 miles across from east to west and 50 miles from north to south (Fig. 2). To the west, Portage Pass at about 700 feet elevation connects Portage Canal in the sound with Turnagain Arm, a branch of Cook Inlet. If it were not for these few miles of land connection, Kenai Peninsula would be disconnected from the mainland. It is this pass, however, that separates the Kenai Mountains from the lofty Chugach Mountains, north of the sound. Elevations in these latter mountains reach to over 13,000 feet while in the Kenai Mountains, the highest peaks are just over 6,000 feet. Glaciers and ice fields cover large portions of these systems. Worthy of note are the Harding Ice Field west of Seward, an unnamed névé to the east, and the interconnected névé north of the sound. Many valley glaciers reach to tidewater; many more terminate a few hundred feet above sea level.

Fiords reach into the mainland from the sound with the forelands jutting out between. These peninsulas are almost continuous in several places with the outlying islands, being separated, however, at the present time by narrow waterways. The largest islands that were probably at one time part of a single preglacial surface are Montague, Hinchinbrook, Knight, and Hawkins. Knight Island is most rugged, having been intensely sculptured by both alpine and piedmont glaciation, and reaches to over 3,000 feet in height.

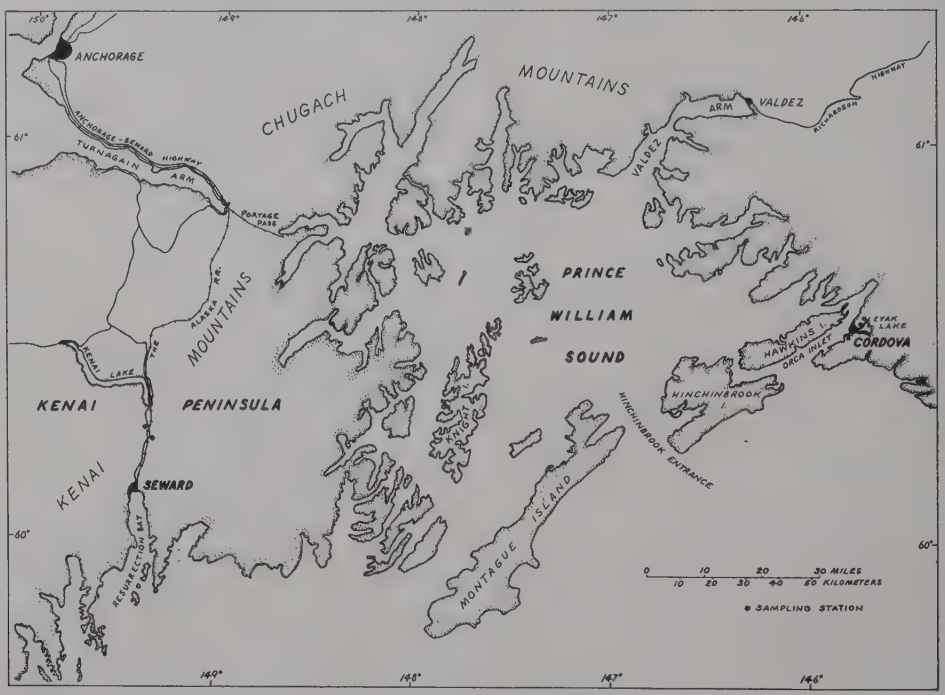

Fig. 2. Sketch map of Prince William Sound and southeastern Kenai Peninsula showing the location of sampling stations in the district.

Montague Island, the largest in the archipelago, is less intensely glaciated while Hinchinbrook and Hawkins Islands appear least affected of the group.

Grant and Higgins (1910a) have divided the bedrock into an older group of slates and graywackes which have been folded, intruded, and partially metamorphosed. The younger group consists of unconformable slates, graywackes, and lesser amounts of limestones and conglomerates. These are also intruded by igneous rocks. The bedrock is commonly blanketed by Pleistocene glacial overburden.

According to Grant and Higgins (1910a), the accordant mountain tops in the region suggest a former peneplain that has since been elevated above sea level and subsequently warped and eroded. Tarr and Martin (1914) have observed rock terraces presently 40 to 100 or 200 feet above sea level which they believe to be remnants of an ancient surface that existed prior to glaciation and not postglacial wave-cut benches that have been uplifted. Evidence for the glacial origin of the sound is founded in part on the submarine topography which shows the deeper and prominent fiords with hanging lateral valleys.

Various workers have recorded the postglacial change of sea level in the region (Grant and Higgins 1910a, Heller 1910, Tarr and Martin 1914, Dachnowski-Stokes 1941, Twenhofel 1952). Submergence of the land, as much as 10 feet vertically, is widespread but discontinuous and local. Vegetation *in situ* and below high tide is being cut by wave action. It is also noted that old beach lines may indicate 3-5 feet of recent elevation, although such evidence of emergence is uncommon.

The immediate district is not one in which vulcanism is known to have occurred. To the northwest of Cook Inlet and Shelikof Strait, however, and along the Alaska Peninsula and on the Aleutian Islands, volcanic action has taken place and has been continuing during postglacial time. Volcanoes in the Iliamna region have been active during the nineteenth century (Martin and Katz 1912) and up to the present. Perhaps the most dramatic eruption was that of Mt. Katmai in the Aleutian Range in 1912, the effects of which have been documented by Griggs (1922). During the 1953 summer, Mt. Spurr in the Chigmit Mountains west of Anchorage erupted. The Wrangell Mountains in the interior to the northeast are also known to represent an active volcanic area.

Glaciation and Nunatak Areas

During the Pleistocene, the intermontane valleys in the Chugach and Kenai Mountains became repeatedly choked by glaciers. This ice found outlets into the interior and toward the ocean. Oceanward, certain ice streams emerged and coalesced in Prince William Sound, forming a broad piedmont glacier which reached into the Gulf of Alaska. The extent of the glacier into the gulf is not exactly known. Middleton Island, situated over 50 miles from the outer islands of the sound, was formerly considered as having been glaciated (Dawson 1893). Recent studies by Miller (1953), however, support a marine origin through deposition from a floating ice shelf, bergs, or both for the material on the island. This glacier, although much larger and projecting into the gulf, was probably similar in many respects to the Bering and Malaspina Glaciers which cover large portions of the southern Alaskan coast at the present time. Tarr and Martin (1914) have shown that the surface slope during the maximum was about 60 feet to the mile between the northern forelands and Hinchinbrook Island. Drowned valleys and basins forming the submarine topography of the sound have been eroded by this ice to depths of 1,200 to 2,400 feet. The largest channel leads from the vicinity of Valdez Arm to Hinchinbrook Entrance. It measures about 40 miles in length and is 7 to 10 miles wide with a depth of 1,200 to 1,500 feet.

The maximum glaciation of the Kenai Mountains was represented by an extensive system of alpine glaciers (Martin, Johnson, and Grant 1915). These glaciers were coalesced but did not override the entire mountain area, thereby behaving unlike a continental ice mass. This ice in part, drained off to the southern coast as well as into Prince William Sound.

Multiple glaciation undoubtedly affected the region of this study. This fact is indicated by the work of Karlstrom (1952) in the upper Cook Inlet area, that of Muller (1952) on the Alaska Peninsula, and that of Krinsley (1952) in southwestern Kenai Peninsula. Four glaciations are recognized in the first two areas and at least three in the latter.

The former extent of glaciation in the sound and on the bordering mainland has been sketched by Tarr and Martin (1914), and although not all of their conclusions regarding maximum ice coverage are based on actual observations, a large portion being conjectural, they have gathered some extremely valuable information on the distribution of unglaciated areas and the manner in which glaciation occurred. They do not, however, specify a multiplicity of glaciation.

Low-lying islands in the sound were completely overridden and nunataks were mainly on the outermost islands. Hinchinbrook Island was not covered completely by ice. A driftless area made

up a large part of this island. Ice along the southeastern slopes which face the open ocean reached to about 400 feet. No evidence of glaciation was found at 440 feet; this end of the island is 1,546 feet at its highest point. Tarr and Martin (1914) suggest that parts of Montague and Hawkins Islands may be driftless. Grant and Higgins (1910a) state that Knight Island in the western sound was not affected by the piedmont glacier above 2,400 feet; they also state that Latouche Island may have been just overridden.

Elsewhere unglaciated areas have been located. Near Alaganik at the Copper River Delta just east of the sound, Tarr and Martin (1914) found no glacial features such as striae in the country rock and erratics in the soil. The western boundary of this unaffected stretch is well-defined while the eastern boundary is less certain. Near Controller Bay further east beyond the mouth of Copper River, Martin River Glacier was only 600-700 feet higher and Bering Glacier underwent little if any extension during ice maxima (Martin 1908). This suggests that the region was only partially covered during at least the last glaciation.

It is unknown to what relative extent glaciers waned during deglaciation in postglacial time. During the present century early observations on their condition were made by several workers (Gilbert 1904, Grant and Higgins 1910b, 1911, 1913, Tarr and Martin 1914); most recent observations have been summarized with the above information by Field (1932, 1937, 1948), Wentworth and Ray (1936), and Cooper (1942). At least a dozen glaciers were advancing in 1935, some attaining positions further forward than at the beginning of this century. Columbia Glacier, which attained its recent maximum between 1914 and 1922, was one of these, although its position in 1935 was behind that reached about 25 years earlier. It is important to note that Columbia Glacier during its most recent maximum had not been further advanced for at least 500 years.

The advancing glaciers of Prince William Sound present a contrasting picture by comparison to the general scheme of recession going on throughout the world. The most widespread recent glacial event recognized in North America is the major recession which generally began during the 18th century; there were also recessions beginning during the 17th, 19th, and 20th centuries, but these were not so widespread. The waxing glaciers in the sound and at several other places in southern coastal Alaska indicate that the late-postglacial surge of ice which has slackened elsewhere is only now reaching its maximum here. The cause for finding receding glaciers side by side with those advancing may be explained by the fact that the level of heaviest snowfall is at present above their fields of accumulation. This has been suggested by Field (1937). Advancing glaciers are favored owing to the location of their nourishing areas at this level. Such an explanation has also been offered for advancing Taku Glacier in southeastern Alaska while other glaciers draining the same ice field have been retreating (Heusser, Schuster, and Gilkey 1954).

The length of post-Wisconsin time must be variable for different localities in coastal Alaska since the time of deglaciation depends on such factors as the location in relation to the terminus of the glacier, the thickness of the overlying ice, the amount of insulation afforded by ablation moraine, the degree of protection offered by topography, and the meteorological condition of the local environment. This lack of simultaneity of the time of deglaciation is illustrated by the behavior of present day glaciers in advancing at one place and receding at another. Because of these variations, post-Wisconsin time can only be an estimate.

As a point of departure for making this estimate, several radiocarbon dates are available (Kulp, *et al.* 1951, 1952). The age of a spruce log near the bottom of a 5-foot, or 1.5-meter (m.), peat section near Boulder Point, Kenai Peninsula, is dated 3,800±400 years old. A sample from the lower foot of an 8-foot (2.4 m.) peat exposure from the north end of the International Airport at Anchorage is given as 5,340±300 years old. What appears to be Mankato—pre-Mankato interstadial material is a 10-inch coaly peat from an exposure on Eagle River north of Anchorage; the radiocarbon age is 14,300±600 years old. More recently Karlstrom (Péwé, *et al.* 1953) has written of the dating of the basal peat of a 16-foot (4.8-m.) section near Boulder Point at 8,200 ±300 years.

These data infer that the last stage of Wisconsin glaciation was manifest between approximately 14,300±600 and 8,200±300 years ago. The length of postglacial time based on the 8,200 ±300 year dating is for the lower part of a 4.8-m. peat deposit. Peat deposits of the study presented here are as much as 3.7 m. deep and one would suspect that the oldest sediments of this section would be somewhat younger than the above figure. In order to test this suspicion, it would be necessary to correlate from the peat and pollen stratigraphy; this cannot be done at this writing, since the radiocarbon-dated sediments have not, as yet, been pollen-analyzed. Until further evidence becomes available, 7,000-8,000

years will be figured as the age of the oldest peat in the study region.

Climate

The climate of this section of coastal Alaska is in large measure a continuation of conditions in the southeast part of the Territory. A comparison of January and July annual average temperatures at Sitka, respectively 32.4° and 54.9° F., with Kodiak, 29.8° and 54.3°, illustrates this point (Kincer 1941). This high latitude coast is tempered by the Japanese current which favors it with a mild climate.

Precipitation declines southwestward and toward the interior as shown by the following average annual figures (in inches): Cordova, 145.4; Valdez, 60.4; Anchorage, 14.3; Seward, 73.7; and Kodiak, 61.5. Autumn months have the heaviest precipitation while spring is generally driest, except at Kodiak where the month of August is driest. Average annual July temperatures are all in the mid-fifties. January averages are warmer toward the coast: Anchorage, 11.2°; Valdez, 19.1°; Seward, 22.4°; Cordova, 27.2°; and Kodiak 29.8° F. These figures show that the study region has January temperatures lower that at Kodiak. Taliaferro (1932) found that mean temperatures in the Controller Bay area were slightly lower than at Yakataga further east. He attributed this variation to the deflection of the current moving up the coast by the islands south of the bay. Such a condition would appear to also have an effect on the sound region.

Vegetation

The Pacific Coast conifer forest prevails in Prince William Sound and at the sampling sites in the southeastern part of the Kenai Peninsula. Elsewhere on the peninsula, components may be found in the valleys and on the lower slopes of the Kenai Mountains, between Seward and Turnagain Arm, and in the southwestern river valleys and coastal areas. Elements of the spruce-birch interior forest are prevalent on the northwest portion of the peninsula (Taylor 1929, Hultén 1941).

The most thorough account of the forests of northern Prince William Sound is given by Cooper (1942). His observations were largely confined to the mainland fiords and borders. The forests of the archipelago within the sound and bordering on the Gulf of Alaska have been observed by Heller (1910). The notes made here, unless otherwise indicated, are taken from the reports of these two individuals.

The arboreal components of the Pacific Coast conifer forest in the sound region number four species. Sitka spruce (*Picea sitchensis*) and mountain hemlock (*Tsuga mertensiana*) are most widespread and abundant, although abundance varies. Generally, mountain hemlock is most common along the fiords in the northern portion while oceanward on the islands, Sitka spruce becomes prevalent. Western hemlock and Alaska yellow cedar frequent the eastern part of the sound and become increasingly uncommon to the west, finally reaching the ends of their ranges.

On Kenai Peninsula, only Sitka spruce and mountain hemlock remain. Stations for western hemlock have been reported on the eastern peninsula bordering the sound, but these are not sufficiently important to warrant more than this note. Sitka spruce occurs furthest along the gulf coast and on Afognak and Kodiak Islands, where its range terminates, it alone forms the forest consociation. Mountain hemlock does not reach further than the borders of Cook Inlet. Distributions for three of the major forest tree species and lodgepole pine (*Pinus contorta*) in Alaska are mapped in Figure 3.

Mature trees in the regional forest average 1-2 feet in diameter with heights of 40-50 feet. Trees with diameters of more than 3 feet and with heights of 100 feet are not commonly encountered; Sitka spruces are most commonly the largest trees. According to Fernow (1902), Sitka spruce attains as much as 5 feet in diameter and 150 feet in height in the Sound region. Numerous dead trees and snags are noticed through much of the forest. These, according to Mr. Clyde Maycock (personal communication) of the U. S. Forest Service in Cordova, are a result of wind damage, subsequent insect infestation, and overmaturity. Timber extends to a maximum of about 2,000 feet in elevation. The limit is lower on certain slopes, but usually not lower than 500 feet above sea level. Trees grow relatively larger in protected places and are restricted in exposed situations.

Blueberry (*Vaccinium ovalifolium*) is the most conspicuous understory shrub. Other important shrub associates are rusty menziesia (*Menziesia ferruginea*) and devils club (*Oplopanax horridus*). Several species of bryophytes and pteridophytes occur near the ground. Seed plants at this level include *Streptopus amplexifolius, Listera cordata* var. *nephrophylla, Coptis asplenifolia, Rubus pedatus, Cornus canadensis,* and *Trientalis europaea* subsp. *arctica.*

Avalanching has prevented stabilization along strips of the forested slopes, and seres frequently do not progress beyond early stages. Alder (*Alnus crispa* var. *sinuata*) often occupies avalanche tracks for many years before slow replacement by

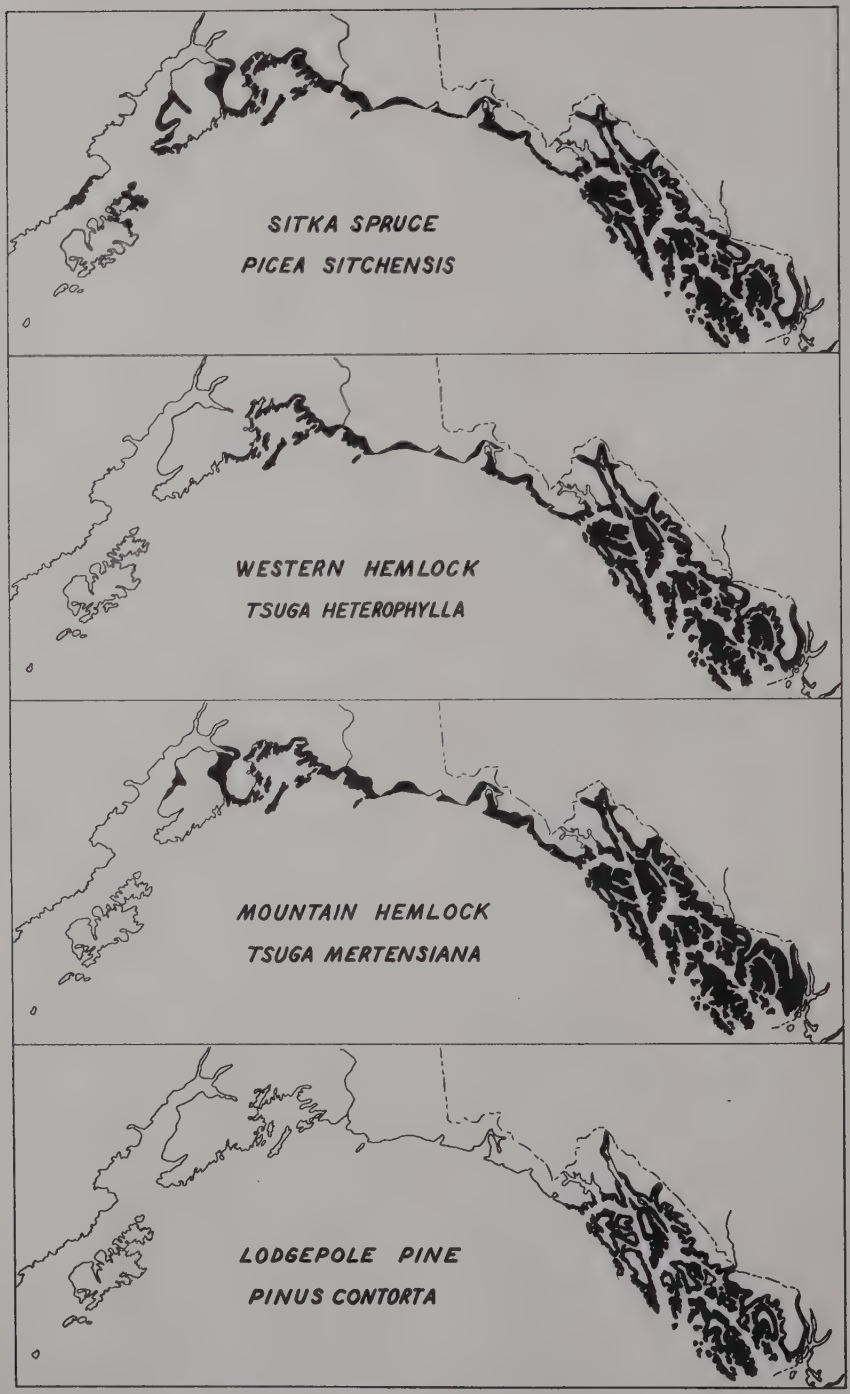

FIG. 3. Sketch maps showing the distribution of some important trees on the southern Alaska coast.

conifers takes place. Seres may begin with dense thickets of lady fern (*Athyrium filix femina* subsp. *cyclosorum*), especially on moist slopes, and later consist of thickets of salmonberry (*Rubus spectabilis*). Currant (*Ribes laxiflorum*) and blueberry (*Vaccinium ovalifolium*) are here intermixed. Along stream courses, hellebore (*Veratrum eschscholtzii*), cow parsnip (*Heracleum lanatum*), and senecio (*Senecio triangularis*) commonly form a "tall herb community." Willows (*Salix barclayi, S. commutata,* and *S. sitchensis*) may mix with alder on open slopes.

A transect study of the sere on outwash is discussed by Lutz (1930). He noted the importance of lupine (*Lupinus nootkatensis*) which as an early invader is invested with the ability to produce nitrogen in the soil, and thus supply this important nutritive element for succeeding plants. Alder, willows, Sitka spruce, and mountain hemlock in his study succeeded almost simultaneously, with poplar (*Populus tacamahacca*) following shortly thereafter. Sitka spruce is preponderant in the climax and associated with mountain hemlock. The composition of the forest climax as well as the plants participating in the succession varies in different places. Lutz's study was made at Sheriden Glacier a few miles east of Cordova. Of interest is the heterogeneity of the plants present on early deglaciated land. Cooper (1942) listed 78 plants which had invaded in less than 21 years from three localities at Columbia Glacier in the northern sound.

Treeless tracts are of three major types. These are also described since their inclusion is pertinent to the discussion which follows concerning the pollen profiles. The first, heath, as a vegetative mat no more than a foot thick, covers comparatively drier situations. Crowberry (*Empetrum nigrum*) is ubiquitous and usually most abundant. Noteworthy associates are the heaths, *Cassiope stelleriana, Phyllodoce glanduliflora, Vaccinium caespitosum, V. uliginosum;* the lycopods, *Lycopodium selago, L. alpinum,* and *L. sabinaefolium* var. *sitchense;* deer cabbage (*Fauria crista-galli*), and the rosaceous *Luetkea pectinata.*

The second, muskeg (called by Cooper, "*Carex* bog"), is also treated by Dachnowski-Stokes (1941) and from personal notes. Muskegs are of two types, sloping (soligenous) and raised or convex (ombrogenous). They have developed under conditions of poor drainage and may contain as much as 15 feet of accumulated peat. Sedges are the commonest plants, but apparently the species vary from place to place. Along the northern border of the sound studied by Cooper (1942), *Carex nigricans* and *C. limosa* formed the principal cover. *Scirpus caespitosus* subsp. *austriacus* and *Carex pauciflora,* by contrast, form the important cover along the eastern forelands and occur on southeastern Kenai Peninsula. Heaths also present are *Andromeda polifolia, Oxycoccus microcarpus, Vaccinium* spp., and *Empetrum nigrum;* other notable plants are cloudberry (*Rubus chamaemorus*), gentian (*Gentiana douglasiana*), and sundew (*Drosera rotundifolia*). It should be noted that muskegs are essentially treeless, although in some instances, low and depauperate hemlocks and spruces can be found growing on them. Lodgepole pine, a tree seen growing as large as 2 feet d.b.h. and 50 feet high on muskegs in the Alaskan "panhandle," is not present in this study district. It reaches the northwestern coastal limit of its range in the vicinity of Icy Point (Fig. 3; also, see Heusser 1954).

Alpine vegetation is the last type of treeless area considered here. Heller (1910) states that the heaths, *Phyllodoce glanduliflora* and *Cassiope stelleriana,* are most characteristic with additional species including *Sedum rosea* subsp. *integrifolium, Luetkea pectinata, Lupinus nootkatensis,* and *Valeriana sitchensis.* An alpine zone extends over a large part of many of the islands, the borders of the sound, and on the peninsula between timber line and existing glacier areas.

In concluding this section, pertinent notes on the tree species are included for a proper evaluation of the pollen diagrams presented later.[2] At the lower latitudinal limit of the coast forest in California, western hemlock and Sitka spruce are low elevation coastal, whereas mountain hemlock grows at high elevations in the Sierra Nevada as a subalpine tree. Climate is mild on the coast and although precipitation is low (dry in summer), the trees thrive under conditions of high humidity in a fog belt. Precipitation is moderate in the Sierra and is largely snow, which on melting during the dry summer supplies moisture during the growing season; summers are mild and winters cold. In Oregon, Washington, and British Columbia, mountain hemlock continues to grow in the mountains away from the coast, and not until Dixon Entrance at the southernmost part of Alaska does it become coastal as well. Over this coastal-timber line range it continues northward. Sitka spruce and western hemlock remain coastal primarily but also reach timber line in the mountains of the Pacific Northwest and mingle with mountain hemlock, Sitka spruce being much more commonly the timber line species.

Near the northwestern terminus of the coast forest, western hemlock is the first to reach the

[2] Alaska yellow cedar is not treated since its pollen does not seem to be preserved in muskegs; no inaperturate conifer grains were encountered in the peats.

end of its range (Fig. 3). The remaining Sitka spruce and mountain hemlock reach timber line in many places together, but the proportion of mountain hemlock along the northern colder and drier border of the sound is much greater than spruce. Sitka spruce is more abundant in the warmer and wetter coastal areas. At Kodiak Island, as the only remaining member of the triad, it has become established quite recently (Bowman 1934, Griggs 1934). Here January and July average temperatures are only 12-13° F. lower than in coastal northern California.

Over the range of the coast forest, Sitka spruce and mountain hemlock become established on both highly organic or mineral soils; although western hemlock also may survive on a mineral substratum, it requires humus soils for greater survival. All three are capable of reproducing in their own shade and are thereby able to perpetuate themselves. This last fact is important in understanding their association in the forest climax.

Location and Description of Muskegs

Peat samples were collected from two muskegs in southeastern Kenai Peninsula. These are situated north of Seward. The first, 12 miles north along the Anchorage-Seward Highway, is near Divide and on the east side of the road above the South Fork of the Snow River at 750 feet in elevation. Almost half the area of the muskeg is open water with several aquatic plants submerged and floating, principally water lily (*Nuphar polysepalum*). Sedges (*Carex* spp. and *Scirpus caespitosus* subsp. *austriacus*), heaths (*Andromeda polifolia, Vaccinium uliginosum, V. vitis-idea, Oxycoccus microcarpus, Ledum palustre* subsp. *decumbens,* and *Empetrum nigrum*), buckbean (*Menyanthes trifoliata*), birch (*Betula nana* subsp. *exilis*), cloudberry, sundew, and pedicularis (*Pedicularis labradorica*) were found growing on the peat. Sitka spruce forest surrounds the muskeg with low mountain hemlock immediate along the margin.

The peat section taken is 1.1 m. in depth with moss composing the upper half and sedge and moss the lower. Microscopic inspection indicated volcanic glass abundant at 0.6 m. and lesser amounts at the decimeter levels sampled below. Structures resembling ascomata of *Microthyrium* (Godwin and Andrew 1951) are also present in the peat. Silt containing pebbles is at the bottom of the section.

The second muskeg is two miles further north beyond Divide at an elevation of 600 feet. It is three miles from the southern end of Kenai Lake and just west of the Snow River drainage. It is essentially flat. A soft and spongy pocket occupies the central portion. There was no open water on the peat. The flora was noted to be similar to that at the first site with the exception of water lily. A similar border of mountain hemlock with Sitka spruce forest beyond encircles the muskeg.

Peat here is 3.7 m. deep. Sedge makes up nearly the whole section with moss mixed in the upper meter and a small amount of woody material stratified between 2.2 and 2.4 m. Two separate portions of the section, the upper half meter and that between 1.4 and 3.0 m., contain volcanic ash. Conspicuous ash layers are at 0.1, 0.2, 0.3, and 1.6 m. *Microthyrium*-like structures and fern sporangia occur at numerous levels. The peat rests on gravel which was difficult to penetrate.

Peat sections from the eastern fringe of Prince William Sound are from near Cordova. All are approximately 200 feet above sea level. Orca Inlet muskeg, one of three studied, is located southwest of the town near the end of Three-Mile Road. It is sloping toward the inlet and covered by herbs except for colonies of mountain hemlock and Sitka spruce with a shrubby undergrowth. Open areas are dominated by sedges (*Carex pauciflora* and *Scirpus caespitosus* subsp. *austriacus*) and heaths (*Empetrum nigrum, Vaccinium uliginosum, Andromeda polifolia,* and *Oxycoccus microcarpus*) with gentian, pedicularis (*Pedicularis parviflora*), and tofieldia (*Tofieldia occidentalis*) also being found. Along the borders of the tree colonies are *Cladothamnus pyrolaeflorus* and rusty menziesia. *Cladothamnus,* a timberline shrub near Juneau in southeastern Alaska, here reaches sea level.

The depth of peat in the muskeg was the least of those in this area. A 1.1 m. section was collected consisting of consolidated sedge with moss remains mixed in the upper half meter. Volcanic shards were observed in all samples with just traces at 0.1 and 0.6 m. Concentrations are at 0.3 and 0.9 m. The material on which the peat rests is composed of both fine and coarse clastics accompanied by cobbles and boulders.

The next deeper section was taken along Seven-Mile Road which follows the north shore of Eyak Lake, east of Cordova. Eyak Lake I muskeg is at mile 4 along the road. It is no more than a hundred square meters in extent and is a combination slope-raised type. The peat, the same as the former in type and stratigraphy, is 1.3 m. in depth. Volcanic ash is present at all levels with the exception of the surface and a decimeter below. Ocher-colored silty sediments mixed with pebbles are at the bottom of the peat.

Deer cabbage, avens (*Geum calthifolium*), and the two sedges mentioned as important at Orca Inlet muskeg prevail. Iris (*Iris setosa*) and skunk

cabbage (*Lysichitum americanum*) were noted as occasional. Sitka spruce and mountain hemlock form the bordering forest.

Eyak Lake II muskeg is at mile 4½ on Seven-Mile Road. Crowberry and the two sedges mentioned for the other Cordova muskegs are the most common herbs. The surface is sloping in the direction of the lake with Sitka spruce and mountain hemlock nearby. The peat is more highly consolidated than at the two previous sites. Mosses are at the surface and associated with sedge remains to 0.5 m., after which sedge continues until 1.1 m. Woody peat begins at this level and alternates with sedge to 2.6 m.; below and to the bottom are only forest remains, well-decomposed and only occasionally containing small chips and twigs. No buried stumps or other wood materials were struck during sampling. *Pediastrum* and fern sporangia were observed in the lower peat. Volcanic ash layers are recorded from nine levels; prominent falls are included at 0.4 and 0.9 m. The country rock basement it at 2.9 m.

Methods

Peat sections were secured with the use of a Hiller borer. This device consists of a 0.5-m. chamber with cutting edge on a 0.5-m. shaft. By means of a handle which is locked into place at the end of the shaft, the chamber may be opened or closed when the instrument has been pushed down into the peat. Turning the handle counter-clockwise opens the chamber and allows the cutting edge to remove a 0.5-m. stratigraphic column of material; turning clockwise closes the chamber. Duraluminum tubular shafts with interchangeable joints based on a design by Lichtwardt (1952) permit sampling the deeper levels with relative ease. Each time the borer was used for sampling, the chamber of the instrument was wiped clean. Peat was carefully removed with a spatula at decimeter intervals in all the sections taken for this study. Samples stored in corked 8 dram shell vials were treated with alcohol preservative as soon as was possible.

Laboratory treatment followed the potassium hydroxide method, using gentian violet stain and mounting in glycerine gelatin. A binocular compound microscope with magnifications of 100x and 440x was used to make the counts. Arboreal pollen (AP) was usually counted to 150 grains. In several instances, lower counts were made; these were in the lower levels of the deeper sections. Counts as low as 25 grains were taken at certain levels. The number of non-arboreal pollen (NAP) was obtained by tallying the non-arboreal grains encountered during an arboreal count. The relative abundance of each type was compared on a percentage basis. Tables I to V show the results of the counts and subsequent comparisons of AP and NAP. Diagrams of the coniferous pollen profiles and the AP and NAP profiles are found in Figures 4 and 5.

Postglacial Vegetation, Climate, and Vulcanism

Mountain hemlock and Sitka spruce were the earliest coniferous trees to occupy the deglaciated land according to the pollen profiles from the deeper muskegs. The degree to which each species prevailed varies, however, during early postglacial time. At Eyak Lake II, mountain hemlock is by far the predominant tree; at Kenai Lake, Sitka spruce[3] exhibits supremacy. This latter section shows the same relative amounts of Sitka spruce and mountain hemlock at the surface as well as at the bottom. Low AP counts at the lower levels relative to high counts at the top indicate that environmental conditions underwent alteration during the intervening time. Another notable feature of this section is expressed by the high proportion of Sitka spruce through the middle third of the section; mountain hemlock percentages are low at this same time. The rise of AP and the decline of NAP coincide with the increase in per cent of Sitka spruce and the decrease of mountain hemlock at mid-section. These trees are the only conifers represented throughout the deposit.

Eyak Lake II section displays essentially the same trends of the Sitka spruce, AP, and NAP profiles found in the Kenai Lake section. Mountain hemlock would also have shown a similarity were it not for the sharp rise of western hemlock in the upper meter. This has altered the mountain hemlock profile following the peak of Sitka spruce in both sections. In general, mountain hemlock which represents 85 per cent of the basal AP, contributes only 45 per cent at the surface with Sitka spruce and western hemlock about equally forming the balance. Western hemlock is scattered by low percentages in the lower two meters of peat (except at a half dozen levels where no grains were counted). The AP and NAP profiles are respectively increasing and decreasing upward by gradual fluctuating steps. At Kenai Lake NAP is over 90 per cent for more than half the lower section; NAP is over 90 per cent for only a small portion of the Eyak Lake II section.

[3] Some of this spruce is possibly white spruce (*Picea glauca*); although this interior species was not observed near the Seward muskegs, Sudworth (1908) has reported it extending to Kenai Lake. This report, however, has not been validated by Hultén (1941-1950).

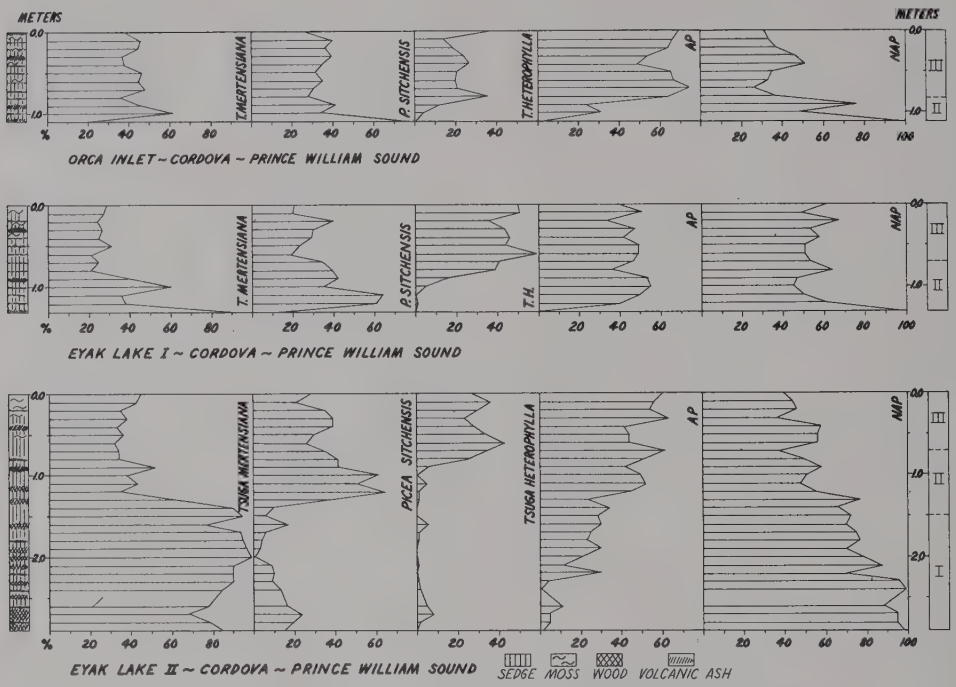

FIG. 4. Peat sections, pollen profiles, and environmental periods for muskegs sampled near Cordova, Prince William Sound, Alaska.

Profiles for Orca Inlet and Eyak Lake I muskegs can be superposed on the upper portions of those from Eyak Lake II muskeg. The NAP profiles from the two former sites are not in complete harmony in their basal portions with the middle part of the latter. This condition is interpreted to be an ephemeral abundance only and associated with the early development of the muskegs; Divide muskeg on Kenai Peninsula also shows a similar high NAP count in the lowest layer.

TABLE I. *Per cent pollen and spores in samples from Orca Inlet muskeg near Cordova, Prince William Sound, Alaska*

	Depth in meters											
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1
Tsuga mertensiana	38	46	45	37	38	47	45	48	36	46	62	22
Tsuga heterophylla	36	14	18	24	27	21	20	21	36	12	4	1
Picea sitchensis	26	40	37	39	35	32	35	31	28	42	34	76
Unknown*	10	6	7	5	11	9	9	6	3	8	3	14
Arboreal pollen (AP)	69	67	63	54	49	65	67	74	64	24	51	3
Polypod	15	21	19	29	12	45	21	28	27	69	46	44
Lycopod	—	—	—	—	—	—	1	—	—	—	—	<1
Selaginella	10	—	—	—	—	—	—	—	—	—	—	—
Cyperad	34	30	53	54	65	21	28	41	20	1	3	—
Lysichitum	—	—	—	—	—	—	—	—	—	—	<1	—
Salix	—	—	—	—	<1	—	—	—	—	—	—	—
Betula	—	4	—	<1	2	—	<1	<1	—	<1	<1	—
Alnus	32	37	25	13	14	26	37	19	27	28	40	55
Empetrad-Ericad	4	3	2	4	4	7	4	2	21	2	9	<1
Cornus	4	5	1	—	2	<1	8	8	4	—	<1	—
Compositae	—	—	—	—	—	—	<1	—	1	—	—	—
Non-arboreal pollen (NAP)	31	33	37	46	51	35	33	26	36	76	49	97

*Number included in original count.

These diagrams stress the importance of obtaining several sections from a given area rather than only one. Cordova diagrams particularly illustrate this point. The first two muskegs sampled, Orca Inlet and Eyak Lake I, were rather shallow. Were it not for discovering the deeper Eyak Lake II muskeg, postglacial vegetational development in the Cordova region would have been incomplete, and conclusions would be based on the shallower muskegs. Of course, where muskegs are few, one cannot choose; where they are frequent, it behooves the investigator to conduct a comprehensive survey in order to obtain as complete a record as possible.

The high percentages of NAP in the lower portions of the Kenai Lake muskeg are contributed by plants which are typical tundra constituents and/or play a role in the early prisere following glaciation (Table IV). Club mosses, ferns, sedges, willows, alders, fireweed, and heaths were some such plants. In protected areas, polypodia-

TABLE II. *Per cent pollen and spores in samples from Eyak Lake I muskeg near Cordova, Prince William Sound, Alaska*

	Depth in meters													
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3
Tsuga mertensiana	29	28	24	27	25	32	22	25	22	41	60	36	38	86
Tsuga heterophylla	50	52	36	43	46	44	59	41	39	16	5	0	1	0
Picea sitchensis	21	20	39	30	29	23	19	34	39	42	35	64	61	14
Unknown*	2	2	5	4	10	9	11	5	5	10	8	3	5	18
Arboreal pollen (AP)	39	51	33	47	42	49	49	47	36	53	55	50	39	1
Polypod	—	—	—	—	—	—	9	26	11	18	17	35	52	79
Selaginella	—	—	—	—	—	—	—	—	<1	—	—	—	—	<1
Cyperad	68	61	82	88	80	73	72	45	60	63	38	11	5	<1
Lysichitum	<1	7	1	8	7	9	3	7	3	2	2	27	4	7
Salix	—	—	—	—	<1	<1	<1	—	—	—	<1	—	—	<1
Alnus	19	22	11	1	10	12	13	18	14	15	25	24	37	13
Betula	2	2	<1	—	1	<1	<1	<1	—	<1	<1	—	<1	—
Drosera	<1	—	—	—	<1	—	1	<1	1	—	—	—	—	—
Empetrad-Ericad	—	<1	1	1	<1	—	—	—	<1	—	—	—	—	<1
Cornus	9	7	4	2	<1	4	<1	3	9	2	16	3	2	<1
Non-arboreal pollen (NAP)	61	49	67	53	58	51	51	53	64	47	45	50	61	99

*Number included in original count.

ceous ferns (probably largely *Athyrium*), fireweed, willow, and alder were the invaders, much in the same way as they are under similar conditions at present. Fern spores are especially numerous in the lower peats of this study; Bowman (1934) also counted numerous fern spores in the peats of Kodiak "bogs," as did Wenner (1947) in Labrador. Fern thickets were probably present in moist places where landslips were taking place. Fireweed occupied the relatively drier outwash as well as moist pockets; it is presumed to be underrepresented owing to its entomophilous nature. Alder and willow also became established near the outset of the prisere, the former succeeding in greater abundance. The unstable terrain undoubtedly brought about the repeated destruction of successional communities while in protected and stable areas where colonies of trees could arise, successions reached their last stage of spruce-mountain hemlock forest. Such wooded tracts occupied a small extent of the deglaciated land. Treeless areas of tundra are considered to have been much more widespread during early postglacial time.

Eyak Lake II muskeg near Cordova may not record as much of the postglacial vegetation, since it is 0.8 m. shallower. Total AP counts of 150 grains were obtained in almost all the lower levels whereas in the lower two meters of Kenai Lake muskeg such counts were difficult to make. Nearby nunatak areas of Hinchinbrook Island, Alaganik, the Controller Bay region, and possibly Hawkins Island were likely covered in part by forest during glaciation and early contributed pollen in greater quantities to the developing Eyak Lake II muskeg. Hinchinbrook Island, for example, according to Heller (1910) is low and forested. Ice did not reach above about 400 feet in the southern island which can reasonably be interpreted as having been below timber line.

The early postglacial climate of southeastern Kenai Peninsula appears to have been more severe for a longer time than that near Cordova. This intimation is drawn from the low AP counts in

TABLE III. *Per cent pollen and spores in samples from Eyak Lake II near Cordova, Prince William Sound, Alaska*

	Depth in meters																												
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9
Tsuga mertensiana	45	43	35	38	33	37	32	33	33	52	38	43	35	64	90	94	77	93	95	97	99	90	90	90	84		78	69	78	85
Tsuga heterophylla	27	36	30	23	28	33	43	33	25	6	—	5	1	1	—	—	6	1	1	0	0	1	0	1	3		5	8	2	0
Picea sitchensis	28	21	35	39	39	30	26	35	42	42	62	51	64	36	10	6	17	6	4	3	1	9	10	9	13		17	23	19	15
Unknown*	9	9	3	5	10	8	7	—	3	6	5	4	2	7	5	6	7	—	2	1	4	3	2	3	11		17	18	15	17
Arboreal pollen (AP)	60	56	54	63	42	44	44	62	51	42	49	52	45	23	34	28	30	25	23	30	21	12	30	4	1		12	5	5	2
Polypod	12	13	35	10	11	24	8	4	14	8	14	13	8	22	13	29	15	23	21	18	24	23	27	14	22		20	9	11	15
Equisetum	—	2	—	—	—	1	1	2	3	1	—	—	—	<1	<1	—	—	—	1	—	2	2	—	—	<1		<1	<1	<1	<1
Lycopod	2	—	—	—	<1	1	2	4	6	4	4	6	—	3	2	2	<1	2	<1	—	2	1	<1	2	<1		<1	<1	<1	<1
Selaginella	1	5	2	1	2	—	—	—	—	<1	<1	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—
Graminad	4	<1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		<1	—	—	—
Cyperad	39	23	17	41	60	24	48	49	44	64	45	52	30	25	25	19	25	14	11	7	8	10	15	1	<1		5	6	4	1
Lysichitum	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	<1	—	23	1	<1	2	<1	—			<1	<1	—	—
Betula	37	7	—	2	1	<1	<1	—	—	1	—	—	3	—	—	—	3	—	<1	—	<1	<1	<1	<1	<1		<1	<1	<1	<1
Alnus	4	38	30	22	—	20	22	20	26	13	27	22	47	39	45	45	53	56	60	46	62	60	50	81	77		72	80	84	83
Nuphar	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	<1		—	<1	—	—
Drosera	—	—	3	—	1	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	<1		<1	—	—	—
Empetrad-Ericad	2	6	10	15	16	20	11	13	2	4	7	4	6	3	1	1	—	<1	<1	2	<1	1	2	1	<1		<1	<1	<1	<1
Epilobium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	<1	—	—
Cornus	—	6	3	8	9	9	6	7	5	3	2	3	6	8	12	4	4	4	6	4	2	2	3	<1	<1		1	<1	<1	<1
Compositae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	<1		<1	<1	<1	<1
Artemisia†	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	<1	<1		<1	<1	—	—
Non-arboreal pollen (NAP)	40	44	46	37	58	56	56	38	49	58	51	48	55	77	66	72	70	75	77	70	79	88	70	96	99		88	95	95	98

NO COUNT

*Number in original count. †Not included in Compositae count.

TABLE IV. *Per cent pollen and spores in samples from Kenai Lake muskeg near Seward, Kenai Peninsula, Alaska*

| | Depth in meters | | |

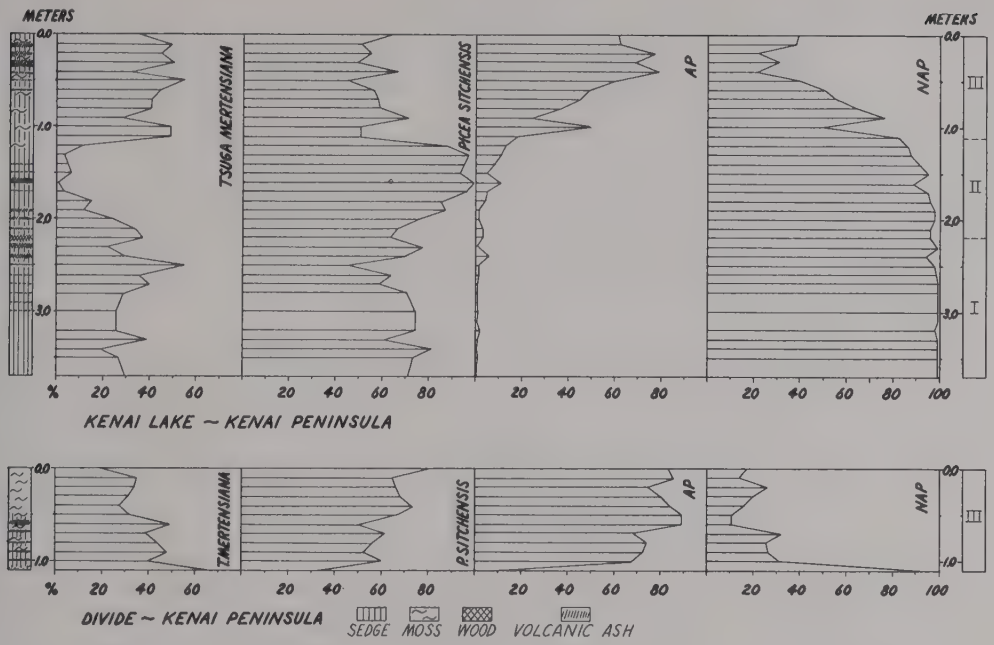

FIG. 5. Peat sections, pollen profiles, and environmental periods for muskegs sampled near Seward, southeastern Kenai Peninsula, Alaska.

tions. Higher percentages of Sitka spruce pollen should possibly not be used as a basis for interpreting greater moisture, since this pollen was probably derived by means of long distance transport from the unglaciated islands of the sound, 75-100 miles distant. As stated earlier AP counts were difficult to obtain in the lower peat. They may then not be representative of the Seward area. The absence of wood peat in the lower section at Kenai Lake may strengthen the evidence for a treeless area as shown by low AP counts. In the absence of trees, non-woody peat would accumulate and render a false impression of greater moisture. NAP counts in both areas would be indicative of cold climate, but moisture may have been variable in the two places at this early time.

A warmer and drier climate succeeded during Period II. Several sources of evidence are available in support of this change. In the pollen profiles, Sitka spruce displays a pronounced peak, mountain hemlock, a trough, and NAP decreases. Wood peat was found in Period II at Eyak Lake II, and although not located during the same period in the shallower Cordova muskegs of this study, Dachnowski-Stokes (1941) describes wood peat in muskegs at Cordova which corresponds stratigraphically with the layer in Period II at Eyak Lake II. No wood was encountered in Period II of Kenai Lake muskeg; the peat, however, showed signs of oxidation and decomposition between the 1.8 and 2-m. levels included in this interval. This warmer and drier time (thermal maximum) has been figured in southeastern Alaska at about 3,500 years from a radiocarbon dating (Kulp, *et al.* 1952, Heusser 1953). No radiocarbon dates are yet available for the period in this district.

Uppermost Period III marked a return of cooler and wetter climate; this most recent episode was probably warmer and wetter than Period I. A suitable environment prevailed which permitted western hemlock to develop and become codominant with Sitka spruce and mountain hemlock. Western hemlock had been unable to expand during Periods I and II, even though it had been in the region. In that AP shows some increase and NAP a certain decrease during Period III, one might argue that this is indication of further warming beyond Period II and possibly an expression of a warmer and humid climate. The decrease of spruce and rise of mountain hemlock would not seem to favor this view. The Cordova climate may have been less affected, since mountain hemlock does not return to predominance in Period III. The contemporaneous rise of western hemlock appears to have masked mountain hemlock, thereby implying an underrepresentation of the latter. It is felt that the change to cooler climate was not sufficiently great to offset the continued rise of AP. The rise of western hemlock,

the change from woody or oxidized peat to sedge peat, the presence of moss remains in the uppermost layers, and the marked development of the shallower muskegs favor a moist climate in late-postglacial time. No conclusive evidence is apparent to indicate a subsequent warming and/or drying as shown in southeastern Alaska by recent decrease of lodgepole pine pollen.

Volcanic ash stratigraphy is also of use in correlating the Cordova and Seward sections and reaching certain tentative conclusions regarding the origin of this material. Such tephrochronological techniques have been applied with considerable success in Iceland (Thorarinsson 1949), in Patagonia and Tierra del Fuego (Auer 1933, Salmi 1941), and in Oregon (Allison 1945, Hansen 1947).

The relative amounts of microscopic pyroclastics were observed in the sections from level to level; these are diagrammed in Figure 6. By first zoning the sections into environmental episodes derived from the pollen profiles, it follows thereafter that the horizons of ejectamenta must be correlated within each episode.

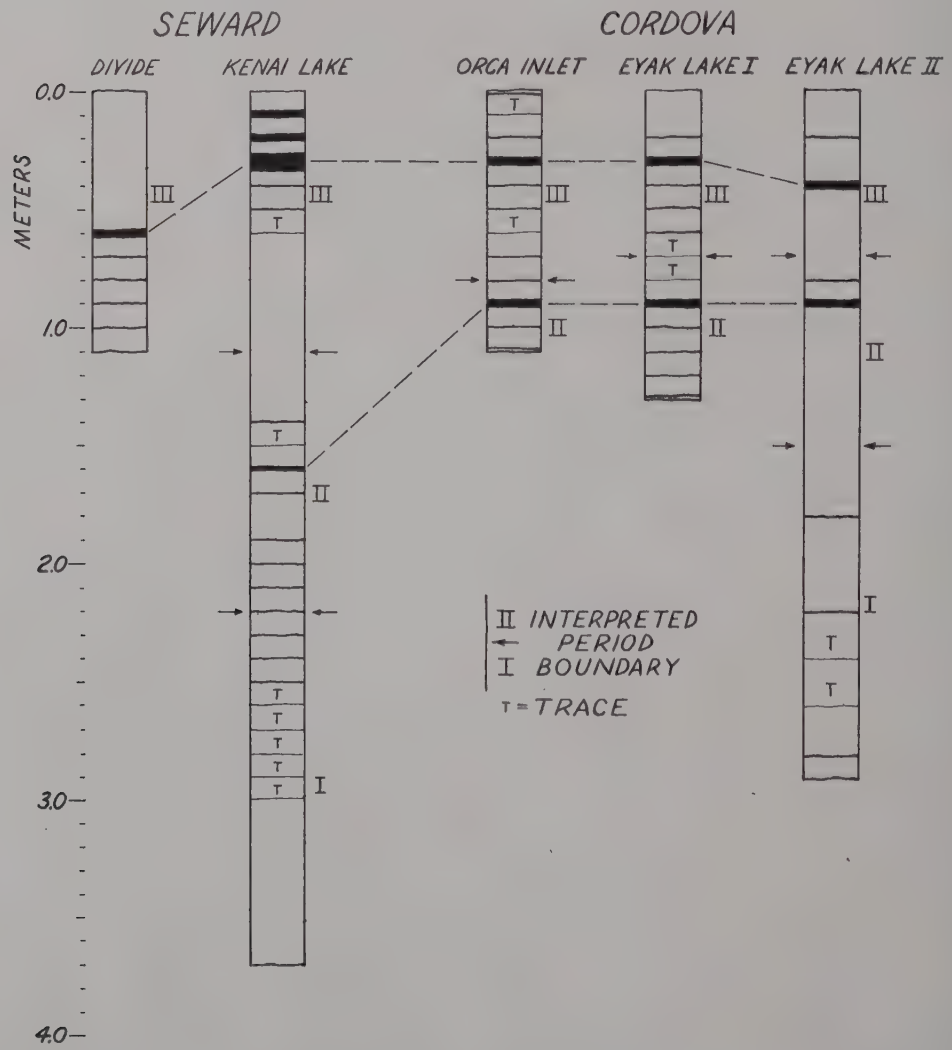

FIG. 6. Muskeg sections from the study district showing the location of volcanic ash strata and their probable correlation.

Two notable ash falls seem to agree stratigraphically. The uppermost is in Period III, the lower in Period II. Seward muskegs contain the greater quantity for Period III, especially the Kenai Lake site which has recorded several successively heavy falls. The single noteworthy horizon at Divide, only two miles from Kenai Lake muskeg, is in need of explanation. A possible interpretation is that all the falls noted in Period III of Kenai Lake were deposited in open water at Divide; sediments were accumulating slowly and were subsequently covered by plant growth during succession and closure of the portion of open water where the section was taken. During burial, no ash was incorporated; peat accumulation then was probably rapid.

The lower prominent layer of volcanic glass present in Period II peat is also distributed in Seward and Cordova sections. Divide section shows no record of this fall as it lacks Period II. Cordova muskegs appear to contain a greater quantity of glass. Ash is contained during Period I, although in very small amounts, and little or no volcanic activity is perceptible in early postglacial time. These observations indicate that activity has been most pronounced more recently.

The greater abundance of ash and numbers of prominent layers in Period III near Seward would imply that the source volcano (or volcanoes) for this material were nearer there than Cordova. The series of "Pilot Charts of the North Pacific Ocean" for 1952, a random year, indicate the wind pattern in a general way for the study district. In view of the winds, as shown by these charts, blowing predominantly from the northwest and southwest during certain months of the year and the volcanic source region in these directions, it can be implied that the ash probably originated in the Aleutian Range. Griggs (1922) has sketched the distribution of Mt. Katmai ash of the 1912 eruption and mentions that as much as ¼ inch fell as far as Katalla (east of Copper River mouth), 400 miles to the northeast. Muller, Juhle, and Coulter (1954) state that a ¼ inch layer of ash was deposited on Anchorage during the eruption of Mt. Spurr, 80 miles to the west, in 1953.

The prominent ash fall in Period II most likely blew from the Wrangell Mountains, 125 miles northeast of Cordova. The quantity of ejectamenta in this layer is greater at Cordova than at Seward. Winds blow down from the Wrangell and Chugach Mountains during many months of the year (Hydrographic Office, 1952). These data would favor this source region; they would also carry the implication that the last major activity in these mountains was during the thermal maximum.

Conclusions

Postglacial reinvasion of the region by plants occurred 7,000 to 8,000 years ago from dispersal loci represented by the islands of Prince William Sound, Alaganik, and the Controller Bay district. Plants survived late-Wisconsin glaciation in these unglaciated refugia. The pollen diagrams, showing mountain and western hemlock and Sitka spruce in the bottom peats, support the contention for the nearness of a pollen source, especially the deepest Cordova section which contains a profusion of conifer grains by comparison to the deepest Seward section. Plants invaded the Cordova region early because of the proximity of the seed source. This is registered by the early-postglacial rise of AP. At Seward such invasion was gradual; AP rise succeeds very slowly. Of interest is a peat section taken from Anchorage, just outside the study region. Hansen (1953) shows that the lower 1.7 m. of the 6.9-m. deposit contains little or no tree pollen. Forests invaded this area extremely slowly and probably largely from unglaciated central Alaska which was a refugium for interior species (Hultén 1938).

Early-postglacial climate under which the tundra formation prospered, gradually improved with the result that forest elements increasingly displaced tundra at lower elevations. Mountain hemlock and Sitka spruce were most active in this cliseral movement while western hemlock, present only in the sound, played a minor role. Sitka spruce reached predominance during the warmer and drier, mid-postglacial interval (thermal maximum). The time of this episode may have been about 3,800 years ago as suggested from the radiocarbon age of the spruce log previously mentioned near the base of the five-foot (1.5-m.) peat section near Boulder Point, Kenai Peninsula. The log may be associated with the woody strata usually representative of warmer and drier climate in coastal Alaska. Its position coincides approximately with the spruce pollen maximum and layers of oxidized peat at Kenai Lake. The age of this log compares with the 3,500-year radiocarbon date for the thermal maximum in the southeastern Territory.

Sitka spruce yielded its superior position during the late postglacial to association with mountain and western hemlock in the sound and mountain hemlock on the southeastern peninsula. These associations have persisted to the present under a cool and moist climate. A trend toward higher percentages in the upper NAP profile at Kenai Lake seems in keeping with the recent cooling.

but it is not of sufficiently long duration to be conclusive.

Glaciers readvanced with the late-postglacial change of climate after having been in a state of retreat during the thermal maximum. A radiocarbon date for wood from the end moraine of Tustumena Glacier in west-central Kenai Peninsula is 400±150 years (Kulp, *et al.* 1952). This age is thought to represent the time the ice readvanced to bury the pre-existing trees from which the dated wood came. It is much younger than the age of interstadial wood at Mendenhall Glacier in southeastern Alaska, dated at 1790±285 years (Kulp, *et al.* 1951). This difference may be a result of variation in the nature and relation of the forests and glaciers of the two areas. The continued advance of glaciers in certain places of the sound and peninsula is in need of explanation.

The postglacial Coast Forest Formation in this northern district developed as an individual unit. The region comprised a locus from which trees could advance into other coastal areas. This advance southwestward to as far as Kodiak Island, as previously noted, has been rather recent. To the southeast, forests are today discontinuous between Prince William Sound and the mainland, northwest of the Alexander Archipelago. Their presence along this stretch of coast is thought to be also a result of recent postglacial migration southeastward from the sound region and possibly also northwestward from south of the limit of the last glaciation in the Puget Lowland of Washington. The large piedmont glaciers in this area, some of which completely cross the coastal plain from the mountains and reach to the Pacific, have acted as obstacles to migration. Malaspina Glacier, for example, reaches the ocean and was formerly of greater size when ice completely filled Yakutat Bay to the east (Tarr and Martin 1914). In addition marine submergence formerly drowned much of the land on which trees are now growing.

Nunataks may have existed between these places whereon trees could have persisted during glaciation and thereby acted as dispersal centers. Dahl (1946) has stressed the point that in areas of high mountains bordering a deep ocean, nunataks are bound to exist. This is so especially on the oceanward side because of the inability of an ice sheet to build up since the ice becomes afloat. Little is known about unglaciated areas along the North Pacific coast of North America, and an intense search may prove such areas to be extant. Antevs (1929), for example, in his reference to the Queen Charlotte Islands to the west of northern coastal British Columbia, states that the northern part of Graham Island, the northernmost member, was not glaciated. Peat sections and pollen profiles from such a region would be exceedingly helpful in completely tracing the spread and rise of this forest from interstadial refugia.

Summary

Five peat sections were collected from muskegs in the vicinities of Cordova on eastern Prince William Sound and Seward on southeastern Kenai Peninsula. The purpose was to reconstruct the regional postglacial vegetation, climate, glacier variation, and vulcanism as a continuation of similar earlier studies on the southeast coast of the Territory.

Prince William Sound is a major embayment of the Gulf of Alaska with Kenai Peninsula bordering to the west. The district was almost completely glaciated by Pleistocene ice; nunataks existed on certain islands in the sound and just east on the mainland. Climate is generally cool with heavy precipitation except at inland stations. Forest and various types of treeless areas comprise the present vegetation. Sitka spruce and mountain hemlock with some western hemlock and Alaska yellow cedar represent the components of the Coast Forest Formation.

Pollen and peat stratigraphy is diagrammed in three successive episodes. Sitka spruce and mountain hemlock were the early-postglacial trees under a cool and moist climate with tundra the predominant formation. Forests became established near Cordova much sooner than at Seward. During the subsequent episode, Sitka spruce reached its maximum when warmer and drier conditions prevailed (thermal maximum). Late-postglacial climate marked a return to a cool and moist environment. Western hemlock became abundant in the sound region at this time while on the peninsula only Sitka spruce and mountain hemlock prevailed. Tundra has been increasingly displaced by coast forest from early-postglacial time to the present. Glaciers readvanced following the thermal maximum; some are still advancing under the existing climate. Volcanic ash layers are also diagrammed and two notable eruptions are indicated and correlated in the sections.

Plants survived glaciation in refugia on nunataks in the sound area which thereby acted as a center for dispersal onto the nearby coasts. To the southwest trees have migrated in recent time; to the southeast, migration has progressed from both the sound and the unglaciated coast of Washington, south of the glacier border. Nunatak refugia may have existed between these places and accordingly acted as additional dispersal centers.

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FLUCTUATIONS IN THE INTERACTING POPULATIONS OF HOST AND PARASITE IN RELATION TO THE BIOTIC POTENTIAL OF THE HOST[1]

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INTRODUCTION

The problem of cyclic fluctuations of insect populations has been approached deductively, starting from the assumption that the fluctuations are inherent in the relation between predator (*e.g.* a parastic wasp) and prey (*e.g.* a host insect). It can be shown mathematically that the interacting species fluctuate in numbers from generation to generation, and the mathematical predictions have been verified experimentally (DeBach and Smith 1941; Utida 1950, 1951a). A further inference from the theoretical model is that the nature of the predator's ecology should influence both the amplitude and the period of the fluctuations, and this was also demonstrated experimentally for certain host-parasite combinations (Utida 1951b, 1953; Takahasi 1953). It is equally reasonable to suppose that the host's ecology should have like effects on amplitude and period. "Ecology" in this context can be considered to be completely embraced by the twin concepts of biotic potential and environmental resistance; in Nicholson's (1933) mathematical approach only the first (the power of increase of the host) was taken into account, but the author (Utida 1953) has shown how both parameters can be allowed for. The mathematical treatment has been published only in Japanese, but a full account in English, together with experimental proofs, is being published elsewhere. For the purpose of the present paper, which reports part of the experimental work, only a brief summary of the theory is needed.

The problem of predator-prey interaction is somewhat simplified, in the case of insect combinations consisting of host and parasite, by the fact that time can be measured in generations, within which mortality is complete. That is, members of one generation do not survive to contribute to the census of the next generation, and the numbers observed in one generation are purely the product of events during the time of the preceding generation. Since this advantage applies to both parasite and host, and since it can be arranged that both species have approximately the same generation time, the approach reduces to a simplified version of the Lotka-Volterra model.

We begin with an expression for logistic growth of either species:

$$N_\tau = \frac{\varepsilon/\zeta}{1 + \{(\varepsilon/\zeta N_0) - 1\} e^{-\varepsilon\tau}}, \qquad (1)$$

where $N\tau$ is the number of individuals at the end of any generation time τ, N_0 is the initial number, and the upper asymptote of population growth (K in the usual notation) has been partitioned into ε, the biotic potential, and ζ, the coefficient of environmental resistance. This is equation (2) of Fujita and Utida (1953), and in this equation it is obvious that neither ε nor ζ depends on the initial number of population N_0. Thus the quantities b and c, defined as

$$b = e^{-\varepsilon\tau}, \qquad c = \frac{(1-b)\zeta}{\varepsilon},$$

are regarded as constants. The total population at the end of any generation is of course $N\tau - \sigma N_0$, where σ is the coefficient of mortality of adult insects in one generation, here taken as 1; letting the

[1] Contribution from the Entomological Laboratory, Kyoto University, No. 224.

total population be P, equation (7) of Fujita and Utida gives

$$P = N_0 \left(\frac{1}{b + cN_0} - a \right). \qquad (2)$$

For the dynamic interaction between host and parasite populations, it is important to realize (1) that intrinsic oscillations are expected in P, even in the absence of the parasite (Fujita and Utida 1953), and (2) that the number of parasite progeny does not increase linearly with the population of adult parasites. Thus the initial density of host population in the $(n+1)$th generation is not the simple product of the final density of the host in the nth generation and the host's power of increase. But, if we assume that equation (2) holds for both species, and that the number of emerged parasites depends on the ratio of parasite and host populations $\frac{P_n}{h_{n+1}}$, we may write equation (2) in the form of simultaneous equations

$$h_{n+1} = H_n \left(\frac{1}{b_h + c_h H_n} - 1 \right)$$

$$P_{n+1} = P_n \left(\frac{1}{b_p + c_p \frac{P_n}{h_{n+1}}} - 1 \right) \qquad (3)$$

$$H_{n+1} = h_{n+1} - P_{n+1}$$

where H_n and P_n are the adult densities of host and parasite populations in the nth generation, h_{n+1}, H_{n+1}, and P_{n+1} are the initial host, final host, and parasite densites in the $(n+1)$th generation, and b and c of equation (2) have been appropriately transformed into b_h, c_h, b_p, and c_p for host and parasite, respectively.

Unfortunately, equations (3) are non-linear difference equations and cannot be solved analytically. In the full version of the theory solutions are obtained by approximative methods with numerical examples, and they are summarized in Table I, with special reference to the modes of population fluctuation expected when the coefficients of biotic potential and environmental resistance of the host are varied through wide ranges. Figure 1 summarizes the same results graphically.

Experimental evidence is given below to support the deduction that in a host-parasite system the amplitude and period of fluctuations of the host population depend on the "ecology" of the host.

Material and Method

As material for the present purpose, we should choose two species of host insect, having a common parasite but differing in biotic potential and in environmental resistance. Since the azuki bean weevil, *Callosobruchus chinensis* (L.) and the cowpea weevil, *Callosobruchus quadrimaculatus* (Fab.), seem to belong to the same ecological niche and to have similar ecology, these species would seem to be unsuitable for the present experiment; on the other hand, they are very suitable in that both are parasitized by a common parasite, *Neocatolaccus mamezophagus* Ishii et Nagasawa, and so it is easy to set up controlled experiments with either host in combination with the parasite. We have therefore chosen these three species, and must perforce work with the relatively slight ecological differences between the two host species.

Two kinds of experimental population are compared with each other; one is the interacting population of *C. chinensis* and *Neocatolaccus* and the other is that of *C. quadrimaculatus* and *Neo-*

Table I. *Mathematical expectation of the relations between the ecological characters of host species and the mode of fluctuations in the interacting population of host and parasite.*

Conditions given		Mode of fluctuations obtained			
Biotic potential of host	Environmental resistance of host	Level of steady state	Amplitude of fluctuation of density	Period of fluctuation of density	Symbol in Figure 1
great	great	relatively low	relatively narrow	relatively long	A
great	small	high	wide	short	B
small	great	low	narrow	long	C
small	small	relatively high	relatively wide	relatively short	D

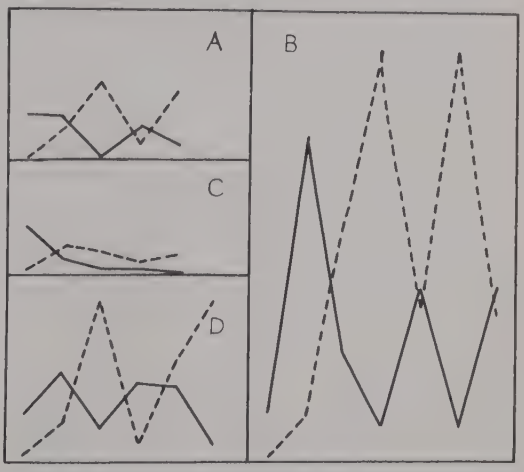

Fig. 1. Types of population fluctuation when the biotic potential and the environmental resistance of host species take different values. (Regarding the symbols in the figure, see Table I.)

catolaccus. As the method used is the same as that of the author's previous experiment (Utida 1950), only a brief outline of it is given here. Twenty grams of azuki bean are used as food for each population, which is maintained in a perti dish of 4.3 cm. radius and 1.8 cm. depth (24.2 cc. capacity). The cultures are kept in darkness at 30°c. and 75% R.H. At each weekly census the adults (male and female) of weevils and wasps are counted, dead as well as living. Food is renewed every three weeks, which corresponds to the time required for one generation of both species of weevil under these conditions.

Since the population fluctuation resulting from interaction of *C. chinensis* and *Neocatolaccus* was fully studied in the author's previous work (Utida 1950), this combination was not repeated, and the previous data are used again. The other host-parasite pair (*C. quadrimaculatus* and *Neocatolaccus*) was studied in two experiments, each being set up in duplicate. In one experiment, small numbers of both host and parasite species were introduced simultaneously at the beginning of the experiment, and in the other a small number of the parasite species was introduced after the host population had attained its equilibrium state.

Results

From the number of dead and living individuals at each census, the number of individuals emerging between two successive counts can be calculated. Since the duration of development of a generation of the weevils is about 3 weeks, the total number of weevils that emerge in a generation is obtainable by summing up the numbers counted in three consecutive censuses. For simplicity, the same treatment is accorded the data for wasps, although some error is thus introduced, the life cycle of the wasp being completed in about 2 weeks. The observations continued about half a year and only eight generations were obtained. Thus the results leave something to be desired, as compared to those for *C. chinensis* and *Neocatolaccus,* which continued for over 50 generations. Figure 2 gives the result of the first experiment, in which *C. quadrimaculatus* and *Neocatolaccus* were introduced simultaneously, and Figure 3 gives the results when the wasp was introduced into a flourishing weevil population.

All four populations show fluctuations, but they differ in detail, even between duplicate experiments. In one of the first experiments (left half of Fig. 2), the host population maintained an almost constant level of density, while the parasite population increased rapidly at first, attaining a high level of density, and then decreased in the 7th and 8th generations. In the duplicate of this experiment (right half of Fig. 2), the fluctuation was at first similar, but after the 6th generation the host population increased gradually while the parasite population fell.

In the other experiment, in which the parasite was introduced after the host population had reached equilibrium, the results of the duplicates are essentially indentical: the parasite increased as the host decreased, but the trend was reversed after the 6th host generation, and the host increased as the parasite population fell.

These fluctuations are very distinct and seem to be due to interaction between host and parasite

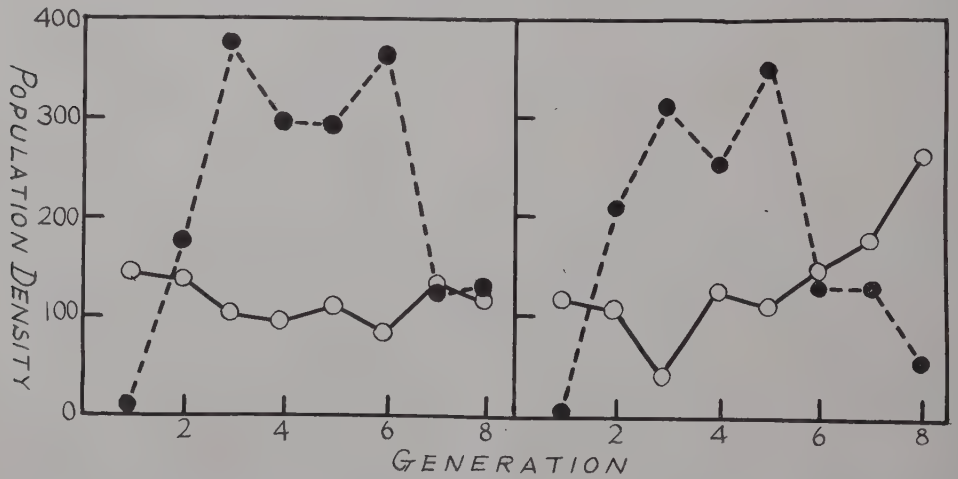

Fig. 2. Population fluctuations when *C. quadrimaculatus* (—O—) is parasitized by *Neocatolaccus* (- - • - -). Both populations of host and parasite start simultaneously.

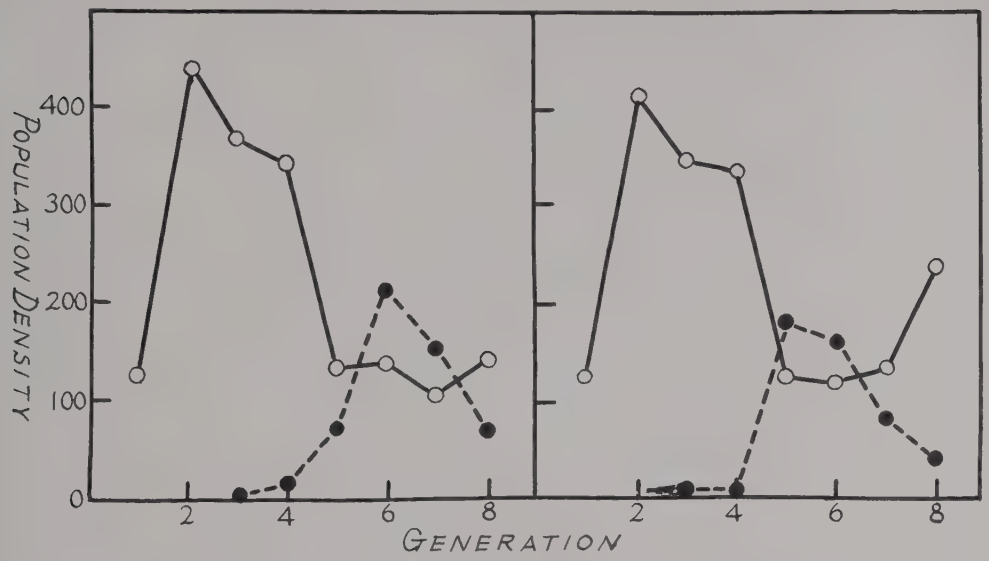

FIG. 3. Population fluctuations when *C. quadrimaculatus* (—O—) is parasitized by *Neocatolaccus* (- - ● - -). Parasite population starts after the host population attains the steady state.

species as predicted by the mathematical theories. The minor differences, *e.g.* those between the duplicate parts of the first experiment, may be attributed to random error but the reciprocal fluctuation in host and parasite populations is clearly reproducible.

We may now come to the comparison between these results and the analogous ones from the *C. chinensis-Neocatolaccus* combination. The interest of this comparison is that *C. chinensis,* though extremely similar to *C. quadrimaculatus,* is known to deposit a slightly smaller number of eggs in an optimum environment (Yosida 1952). This would mean that its biotic potential (ε in equation (1)) is slightly smaller, and, as Table I shows, a species with a smaller potential should not give such violent fluctuations in numbers when it lives with its parasite. Results for *C. chinensis,* the species with the smaller biotic potential, are given in Figure 4, which is reproduced from the author's previous paper (Utida 1950), and, as may be seen, the amplitude and period of the fluctuations of the host population are smaller than those for *C. quadrimaculatus.* That is, particularly in respect to amplitude, the difference between the experimental results (comparing especially the right half of Fig. 2 with Fig. 4) is like the difference predicted theoretically (comparing A with C or B with D in Fig. 1). On the other hand, in respect to the absolute density attained by the host species at equilibrium, the results are not so clear-cut; at least, while there appears to be a slight difference in favor of the species with the higher potential (Fig. 2, especially the right half), the difference is not obvious in the relatively short span of available observations, and may not be significant.

If the theory is only partially verified by this comparison, it may be because of unconsidered variations in ζ, the coefficient of environmental resistance. We have assumed that ζ remains constant, as seems reasonable when the major deterrent to potential increase of the weevils, the presence of the wasp, is the same for both species. However, this may not be correct, and since variation of ζ will have an influence on the mode of population fluctuations that is of like magnitude

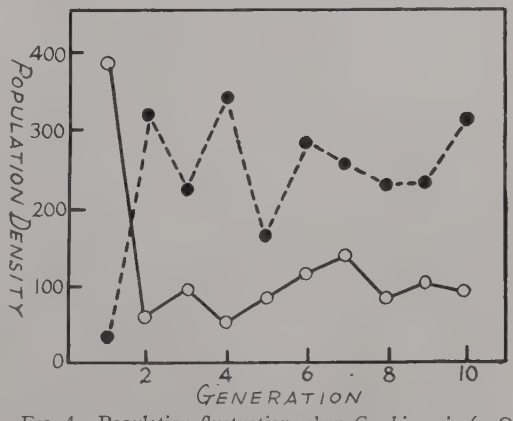

FIG. 4. Population fluctuation when *C. chinensis* (—O—) is parasitized by *Neocatolaccus* (- - ● - -) (from Utida 1950).

but opposite sign to variation of ε, different experiments will have to be designed to test this possibility. For the present, we conclude that the amplitude of the fluctuation in host and parasite populations is dependent on the intrinsic rate of increase of the host population. This conclusion is the same as that deduced mathematically by Nicholson (1933) and the present author (1953).

The author wishes to express hearty thanks to Dr. E. S. Deevey of Yale University for reading through his manuscript and polishing its style.

Summary

When the cowpea weevil *Callosobruchus quadrimaculatus* is maintained in controlled conditions with its parasite, the wasp *Neocatolaccus mamezophagus,* reciprocal fluctuations of numbers are observed in host and parasite. A similar result was obtained earlier with another species of weevil, *C. chinensis,* in interaction with the same parasite and in identical conditions of culture. The mode of the fluctuations is not quite identical in the two host-parasite combinations, however, the amplitude being greater when the host is *C. quadrimaculatus.* This difference is attributed to the slightly greater biotic potential that *C. quadrimaculatus* is known to have, for it can be shown theoretically that the amplitude of population fluctuation depends in high degree upon the reproductive potential of the host species.

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WATER RELATIONS IN TWO SPECIES OF TERRESTRIAL MOSSES

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As every bryologist with field experience knows, there is a sharp correlation between the occurrence and distribution of many species of mosses and the conditions of moisture of the habitat. As in vascular plants, most species can be grouped ecologically into xero-, meso-, and hydrophytes. Little is known, however, concerning water relations in the moss plant itself, so that interrelationships of structure, physiology and habitat are not well understood.

It is rather generally accepted that rhizoids are not responsible for much, if any, water absorption and that in most mosses only negligible amounts are translocated internally. Water obtained by the moss plant from the substrate is presumed, therefore, to rise by capillary movement on the outside of the plant. Atmospheric moisture is absorbed directly through the leaves and stems either in liquid or vapor form or both. Corticolous and rupestral mosses presumably obtain water principally from the atmosphere while terrestrial mosses are generally assumed to absorb water from both soil and atmosphere. The present study on two species of terrestrial mosses, *Atrichum angustatum* Brid. and *Polytrichum commune* Hedw., was made in an attempt to determine and compare the relative amounts of water these species absorb, (1) from the substrate, and (2) from the atmosphere. Such information might be useful in explaining the distribution of mosses according to conditions of moisture.

Apparently most of the early investigators assumed that water conduction in mosses takes place entirely in the central strand of the stem and some even went so far as to refer to this structural feature as "the conducting strand." Bowen (1931, 1933), however, in a series of ingeniously devised experiments, demonstrated conclusively that

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water is conducted almost entirely over the external surface of the stem. Mägdefrau (1937) obtained similar results in experiments with several species of mosses. The central strand serves only as supportive tissue. Bowen (1933) observed that water absorption takes place through the leaf-bases and leaf-traces, especially through the thin-walled cells at the tip of the plant. Her investigations included 22 species, ranging from submerged aquatics to extreme xerophytes. For each species, she determined the height and rate at which water moves externally over the stem but no quantitative measurements were made of the amounts of water reaching the stem tips. Thus, there is no evidence that water can be transported externally from the substrate to the tip of the stem in sufficient quantities to permit growth in such tall mosses as *Polytrichum commune*. Müller (1909), for example, reports that the tops of *Rhodobryum roseum* remain dry after the bases of the stem have been immersed in water for as long as 18 hours and in several species of the *Hypnaceae* water rises to a height of 5 mm., but does not reach the tips of the stems. Similar observations have been made by Plantefol (1927) on *Mnium undulatum* and *Polytrichum formosum*.

Investigations on the absorption of water from the atmosphere by mosses have been somewhat more numerous. Liquid water is absorbed rapidly and in considerable amounts when an air-dry moss is submerged in water or is exposed to a supersaturated atmosphere. Certain species of *Sphagnum* can absorb 16 to 26 times their own dry weights (Lesquereux 1847, Düggeli 1903, Paul 1908, all cited by Müller 1909). According to Müller (1909), the corresponding values would be 3.1 for *Polytrichum commune*, 6.4 for *Hypnum cuspidatum*, and 7.1 for *Anomodon viticulosus*. The same author found that after an exposure of one second to a supersaturated atmosphere, *Rhodobryum roseum* absorbed water to the extent of 23% of its dry weight and after 5 seconds *Hypnum cuspidatum* absorbed 77%. *Hypnum* [*Rhytidiadelphus*] *triquetrum*, when immersed in water, reaches its maximum water content (150 to 200 parts for 100 parts of dry matter) after 15 minutes (Plantefol 1927). The magnitude and rapidity of absorption of liquid water in mosses is apparently due to the widespread lack of cuticularization in leaves and stems of most species (Vaizey 1887, Czapek 1899, Kressin 1935, Patterson 1943).

Water vapor, as would be expected, is absorbed to a far lesser degree and much more slowly than liquid water. Species of *Sphagnum* can absorb only 10 to 33% of their dry weights of water from a saturated atmosphere (Oltmanns 1884, Düggeli 1903, cited by Müller 1909). Müller (1909) determined the amount of water absorbed from a saturated atmosphere at constant temperature by various inert substances and living organisms. The former included sand, humus, limestone, and filter paper, while for the latter he used seeds, mosses, and liverworts. He found that at saturation the water content of the mosses studied varied from 30.3% to 58.2%. In contrast, the filter paper, composed of pure cellulose, contained only 18%. Müller found no significant differences in water absorption between living and dead moss plants. From these results he concluded that absorption is a purely physical process and that substances other than celluloses were involved, presumably hemicelluloses. Plantefol (1927), after an extensive study of water relations in *Hypnum triquetrum* also concluded that only physico-chemical forces such as capillary and imbibitional forces were involved in water uptake. He pointed out that water held by imbibitional forces in the moss plant has a vapor tension which is in equilibrium with the atmospheric vapor tension. For example, when the relative humidity is 95% at 14° C., the water content of *Hypnum triquetrum* is equal to 50% of the dry weight, while at 70% relative humidity, the water content is only 27% of the dry weight. Patterson (1943) made similar determinations of the amounts of water absorbed at various levels of atmospheric humidity by mosses from xeric, mesic, and hydric habitats but he was unable to find any correlation between the magnitude of the absorption and the type of habitat in which the mosses usually grow. Clausen (1952) measured rates of evaporation in a large number of hepatics and, although she found that some dried out faster than others, there was no correlation between rate of drying and the distribution of species in nature.

In the present study, two species of terrestrial mosses were selected, both belonging to genera in the family Polytrichaceae. *Polytrichum commune* is found in nature in habitats with a very wide range of moisture conditions, from permanently wet to damp and, less frequently but not uncommonly, in moderately xeric situations. Gametophytic plants commonly reach 10 to 20 cm. in height and in wet boggy places as much as 30 to 40 cm. The leaf has a long broad leaf-base which sheaths the stem and narrows abruptly into a tapering limb. The angle of divergence of the leaves is related to the water content of the plant. When air-dry the angle is almost zero and the leaves are closely and imbricately appressed to the stem or at most only the extreme tips of the leaves are spreading. When wet, the

leaves are widely spreading, often recurved and the leaves diverge at right angles or more. As plants dry out, the angle of divergence of the leaves with respect to the stem decreases. The water balance can thus be estimated in a general way by observing the relative angle of divergence of the leaves. *Atrichum angustatum* likewise grows in a wide variety of situations from wet to dry, although it is found more commonly in mesic to xeric habitats. Its maximum height is considerably less than that of *Polytrichum commune,* which was one of the reasons for selecting it for study. *Atrichum angustatum* occasionally reaches 4 cm. in height in moist places, but in mesic or xeric sites it rarely exceeds 1 to 2 cm. The leaves lack a sheathing base and when dry are crispate, *i.e.,* curled and twisted. When moist, the leaves are erect and spreading as in *Polytrichum.* Similarly the degree of curling and twisting is related to the moisture content of the plants.

The mosses were collected with an attached layer of soil about one inch thick and taken to the laboratory where the temperature was maintained at approximately 26° C. Atmospheres of constant moisture content were established in desiccators or under bell jars by using mixtures of sulfuric acid and water in various proportions. An atmosphere of zero humidity was obtained by using calcium chloride. Observations were made on the absorption of liquid water from the substrate and on the absorption of liquid water and of water vapor from the atmosphere.

Absorption of Liquid Water from the Substrate

Clumps of both *Polytrichum* and *Atrichum* were cut out approximately 6 x 6 cm. square with the one-inch thick soil layer still attached to the plants. The clumps were placed in open glass dishes and air-dried for a period of at least a week, at which time the water content of the mosses was assumed to be at equilibrium with the atmospheric moisture (Plantefol 1927). As water is evaporated from the plants, the leaves of both species gradually lose their turgescence and become either appressed or shrivelled according to the species. Water was then very carefully poured into the dishes in a manner that would not permit any liquid water to come into contact with the above-ground parts. The water level was brought just even with the soil line. The soil was thus saturated. In *Atrichum,* the lower leaves began to expand and regain turgescence almost immediately and there was progressive recovery up the stem. The leaves at the tip of the stem were the last to unfold. There was considerable variability in the length of time required for water to reach the tips of stems in different clumps which was due apparently to differences in the compactness of the soil and to the closeness of the plants in the clump. In general, the more compact the plants, the faster water reached the tips. Complete recovery, however, was attained in all clumps of *Atrichum* within 2 to 3 hours.

Similar treatments with *Polytrichum commune* produced different results. Within a few hours after the water was added the lower leaves of this species showed evidence of recovery and for a few centimeters beyond there was partial recovery of leaves. After 5 weeks, however, the leaves in the upper 5 cm. of the plant still showed no evidences whatever of even partial recovery. No significant differences were noted between plants which were kept in 95% humidity and those which had been exposed to laboratory atmosphere, where the humidity averaged 65%. To obtain complete recovery of the leaves at the tips of the stems of *Polytrichum,* it was necessary to raise the water level to within 1 cm. of the tips of the stems.

When the aerial parts of both *Atrichum* and *Polytrichum* are totally immersed in water they recover within a few minutes. There is similar recovery when water is sprinkled on the tips either with a sprayer or atomizer. These conditions would simulate natural occurrence of rain, dew, and possibly fog.

Absorption of Water Vapor

The aerial parts of both species were placed in a series of bell jars with atmospheres adjusted to various relative humidities. Plants were allowed to remain for a period of 5 weeks. Neither of the species achieved complete turgescence in any of the humidities supplied. Plants in 100% humidity for 5 weeks failed to absorb sufficient water to cause leaf expansion.

A second series of observations was made on plants of both species in which the aerial parts were first soaked in water so that the leaves were fully expanded and turgescent. They were then placed in a series of bell jars with varying atmospheric humidities. At the end of 5 weeks, the leaves of plants of both species were distinctly "wilted" in all humidities up to and including those in 95%. The rate of "wilting" was, as would be expected, inversely proportional to the relative humidity, those in the low humidities "wilting" first and so on. Even at 100% relative humidity, however, all of the plants of *Atrichum angustatum* definitely showed the crisped condition. On the other hand, plants of *Polytrichum commune* at 100% still indicated slight divergence of the leaves at the end of the five-week period.

This is probably related to the fact, as will be shown below, that on a dry weight basis relatively more water is required to maintain turgescence in *Atrichum* than in *Polytrichum*.

The moisture content of both species was determined as nearly as possible at the time that leaves began to show the slightest signs of "wilting." Plants were washed thoroughly, the excess water allowed to drain off by gravity and were then exposed to laboratory atmosphere. At the first sign of shrivelling, plants were picked individually, placed in tight weighing bottles and weighed individually. They were then oven-dried (48 hours at 105° C.), reweighed, and the moisture content calculated. The weights for each species were averaged and the following results were obtained:

	Moisture content at the point of "wilting" (percentage of dry weight)
Polytrichum commune	85.5
Atrichum angustatum	109.5

These figures are reasonably constant regardless of the humidity level of the surrounding atmosphere.

To determine the moisture content of plants of the two species when they are in equilibrium with different levels of atmospheric humidity, the following procedure was employed. Aerial parts of the two species were first air-dried in laboratory atmosphere and then placed in atmospheres of various constant humidities between 0% and 100%. At the end of 8 days, plants were removed and the moisture contents determined as previously outlined. The average water content for each level of humidity for both species in terms of percentage of oven-dry weight is presented in Table I and is graphically shown in Fig. 1.

TABLE I. *Water content of moss plants at different relative humidities*

	0%	38%	68%	85%	90%	100%
Atrichum.....	14.3	16.0	10.4	31.9	....	91.5
Polytrichum.....	12.2	14.0	21.7	43.3	44.9	85.7

One difficulty in evaluating these data, as with those obtained by previous investigators (*e.g.*, Bowen 1933, Roberts and Haring 1937, Patterson 1943, etc.), is that moisture contents are indicated solely in terms of percentages of the dry weights of the plants. It is not very meaningful, therefore, to compare moisture content values of one species with those of another because, for structural or other reasons, some species require relatively more water to bring them to turgescence than others. As already pointed out, mosses are poikilohydrous, *i.e.*, the water content fluctuates with the relative humidity of the atmosphere. The ecological significance of the water content at various humidities must be considered in terms of growth and survival of the moss plant. Growth is generally assumed to take place only when plants are fully turgescent, although this is a point that needs further investigation. It is suggested, therefore, that water content at various humidities would be more meaningful if it were expressed in relation to the water content of turgescent plants. The difference between the water content at turgescence and the water content at various relative humidities can be termed the water deficit, which can be expressed as a percentage of the water content at turgescence. Water deficit is thus the amount of additional water that a moss plant would have to absorb to become turgescent, with the leaves fully expanded and straightened out. It can be expressed as follows:

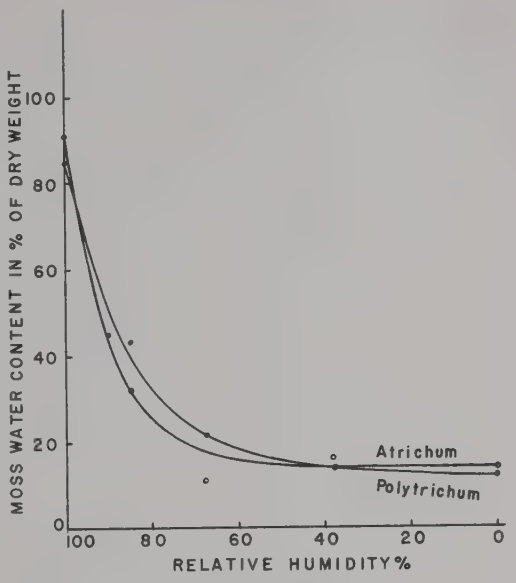

FIG. 1. Water content of *Atrichum* and *Polytrichum* in relation to relative humidity.

$$\frac{\text{Water content of turgescent plants} - \text{Water content at a given humidity}}{\text{Water content of turgescent plants}} \times 100 = \text{Water deficit}$$

For example, at 100% humidity the water content of *Atrichum angustatum* is 91.5% of its oven-dry weight. Its water content, however, when the leaves are turgescent is 109.5% of its oven dry weight. Thus,

$$\text{Water deficit} = \frac{109.5—91.5}{109.5} \times 100, \text{ or } 16.4\%$$

On the other hand, in *Polytrichum commune,* at 100% humidity:

$$\text{Water deficit} = \frac{85.5—87.5}{85.5} \times 100, \text{ or } 0\%.$$

The water deficits for the respective humidities are shown for each of the two species in the following table (Table II) and graphically in Figure 2.

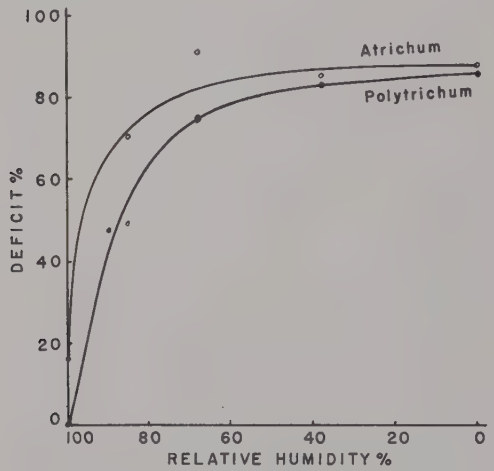

FIG. 2. Water deficit in *Atrichum* and *Polytrichum* at various levels of relative humidity.

TABLE II. *Water deficit of moss plants at different relative humidities*

	0%	38%	68%	85%	90%	100%
Atrichum.....	86.9	85.4	90.5	70.9	....	16.4
Polytrichum.....	86.0	83.6	74.6	49.4	47.5	0

Stocker (1929) has used the expression, saturation deficit, to describe the water balance in the leaves of higher plants, but he expressed the deficit as a percentage of the maximum water content of fully turgid leaves. It is more difficult to determine the water content of moss plants when they are precisely at saturation. Immediately after soaking in liquid water, the plants contain water in excess of saturation. This can be removed by blotting with filter paper, shaking or other similar means but it is difficult to standardize such procedures and determinations are thus very inconstant. For this reason, in the present study, after soaking, the excess water was allowed to drain off by gravity and weighings were made when plants showed the first signs of "wilting." The measurements were thus made when the plants were just shy of saturation and the figures are slightly less than the values for true saturation. This procedure makes it possible, however, to obtain rather consistent values.

DISCUSSION

The data presented here confirm the observations of Müller (1909) and Plantefol (1927) that erect-growing mosses of any appreciable height (more than 2 to 3 cm.) cannot absorb sufficient moisture from the soil to produce or maintain turgescence. This is contrary to the conclusions of Bowen (1931) that ". . . the amount of water so conducted is large and sufficient to maintain the plant in a healthy condition." She found that water can be conducted on the outside of the stem of *Polytrichum* to a height of 17 cm. Her measurements of the volume of water transported, however, were made by placing plants in solutions of sodium chloride, determining the amount of salt accumulation on the entire plant after 8 days and then calculating the volume of water that would had to have risen to deposit the amount of salt found on the plants. On this basis she found, for example, that in the course of a week as much as 8 c.c. of water passed over the surface of a single plant. She did not distinguish quantitatively, however, between the amounts of salt at the tip of the stem and at the base.

Mägdefrau (1937), reports that plants of *Polytrichum commune* remained fresh and turgescent when kept at a humidity of 70%. Unfortunately, Mägdefrau does not mention the height of the plants used in his experiments nor the distance from the water level to the tips of the plants. Plants of two other genera, *Thamnium* and *Rhytidiadelphus,* did not remain turgescent, however, at either of the humidities. Both of the latter have distant leaves which, according to Mägdefrau, are too far apart to facilitate external conduction of water in sufficient quantities to maintain turgescence. Some of the discrepancies among the results of different investigators on the same species of moss may be due to the fact that they are using experimental plants with widely varying leaf distances.

It has not been determined to what extent mosses can grow when the leaves are in a shriv-

elled or "wilted" condition. Davy de Virville (1927) observed complete stoppage of growth in several species which were kept in very moist soil in pots at atmospheric humidities of 65% to 80%. Plantefol (1927) reports very low values of photosynthesis and respiration for *Hypnum triquetrum* when the moisture content is below that which is required to maintain turgescence. Several cytological investigators have pointed out that it is necessary to keep the gametophytic plants of mosses moist and in a turgescent condition in order to obtain mitotic division figures for chromosome studies (Heitz 1942, Lowry 1948, Virginia S. Bryan, unpublished). The assumption, therefore, that growth in mosses takes place only when the plants are in a turgescent state is probably a valid one.

Soil moisture would seem to be of ecological importance in mosses mostly if not entirely in the early establishment of plants on the site, *i.e.*, during germination of spores, gemmae and propagula, protonemal development and the early growth of the gametophytic plants. After plants attain a height of one to two cm., apparently sufficient moisture cannot be conducted from the soil to maintain plants in growing condition. Furthermore, observations on the uptake of soil water have been made when the bases of the plants are in liquid water. No observations are available on absorption from soils that are at or below field capacity, but the amounts absorbed under these conditions could be assumed to be much less than from soils above field capacity. Clausen (1952) observed that hepatics growing on highly porous substrates lose water to the substrate if there is a vapor pressure deficit in the latter.

The important source of water for the growth of mosses must then be actual precipitation in the form of fog, dew, or rain. Even the effectiveness of fog and dew, however, may not be as great as generally supposed if Clausen's (1952) observations on hepatics are applicable. She found, for example, that in the early morning following either heavy dew or fog hepatics which are sheltered in any way by taller vegetation are not turgescent. Only those species growing in open and unsheltered places regain turgescence during a night's heavy dew or fog. But, as Clausen points out, those plants in open places shrivel within a few minutes after the sun emerges. Assimilative processes under these conditions would be of extremely short duration and only prolonged periods of this nature would be effective in promoting growth.

Summary

1. Water relations in two species of terrestrial mosses, *Polytrichum commune* and *Atrichum angustatum,* were studied with respect to absorption of liquid water from the soil and atmosphere. Qualitative and quantitative measurements were made on the absorption of water vapor from the atmosphere.

2. Liquid water can be conducted only for distances of 1 to 2 cm. up the stem in qualities sufficient to produce turgescence in the leaves of the mosses studied.

3. Aerial parts of both species fail to absorb sufficient water vapor from the atmosphere to regain turgescence even when kept at a relative humidity of 100% for as long as 5 weeks.

4. The water content of mosses which is in equilibrium with various levels of atmospheric humidity can best be expressed in terms of water deficit, which describes the actual water balance of the moss plant.

5. The water deficit for each species was determined at various levels or relative humidity between 0% and 100%. At all humidities the water deficit was greater in *Atrichum* than in *Polytrichum.* At 100% humidity there was no deficit in plants of *Polytrichum,* but in *Atrichum* the water deficit amounted to 16.4% at 100% humidity.

6. It is concluded that water precipitation in the form of fog, dew, and rain, but mainly the latter, is the only effective source of water for the growth of mosses.

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THE POPULATION DYNAMICS OF CONFINED HOUSE MICE SUPPLIED WITH UNLIMITED FOOD[1]

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INTRODUCTION

This is the second in a series of studies undertaken at the University of Wisconsin to analyze the factors involved in the growth and regulation of house-mouse (*Mus musculus* L.) populations. Strecker and Emlen (1953) measured the growth and behavior of confined house-mouse populations living with a restricted food supply. They analyzed the role of food in population ecology. The present study was designed to investigate cover and space as other important factors influencing population behavior. Mouse populations in this study were confined in large pens but given unlimited food and water to determine at what level and by what mechanism the populations would be limited.

House mice are excellent subjects for experimental studies of mammalian population phenomena since they occur naturally in buildings, have relatively small home ranges, and possess a rapid life cycle which insures the acquisition of data in a reasonable length of time.

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METHODS

Six experimental populations of house mice were each established in a pen 6 feet wide and 25 feet long. Each pen contained 48 nest boxes, 2 x 3 x 6 inches in dimensions, and an abundance of food, water, and nesting material. The pens were lined with sheets of galvanized iron 24 inches high, which effectively confined the mice.

On November 22, 1950, 4 pairs of healthy young adult house mice, which were wild-trapped from natural infestations on the University of Wisconsin campus, were released into each of the pens. Each pen received the same amount of food and nesting space, but in three of the pens (designated A, C and E) the nest boxes were crowded at one end and the food and water were placed in large containers at the opposite end. In the other three pens (B, D and F), the nest boxes were widely dispersed around the two long sides of the pens, and the food and water were placed in 24 bowls down the center of the pen (Figs. 1-4).

The populations were permitted to grow undisturbed except for routine handling (minor exceptions in two pens will be noted later). All nest

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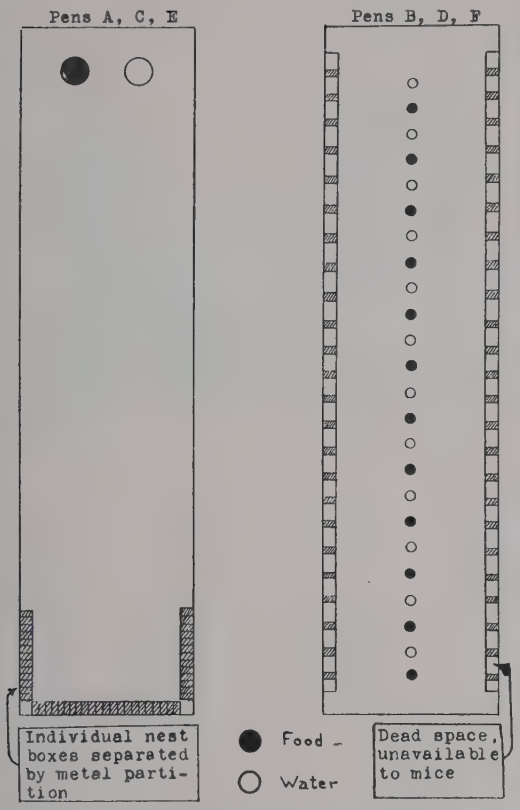


FIG. 1. Floor plans of pen types. Shaded areas represent nest boxes. Circles show location of food and water bowls. Dimensions of each pen are 25 feet by 6 feet.

FIG. 2. Photograph of Pen A representing concentrated housing conditions. Pens A, C and E were identical.

boxes were examined at two-week intervals, and every four weeks all the animals were caught, weighed and externally examined for health and breeding condition. During these census checks, all litters, dead or alive, were noted and their dates of birth were estimated by age criteria given

FIG. 3. Photograph of Pen C showing concentrated feeding conditions. Pens A, C and E had the same type of food and water facilities.

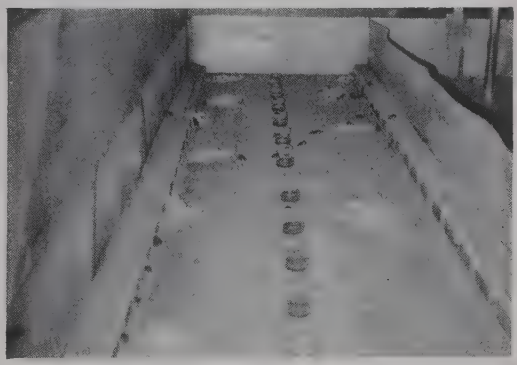


FIG. 4. Photograph of Pen D representing dispersed food and housing conditions. Pens B, D and F were identical.

in Snell (1941). Young were individually marked as soon as their eyes were open by clipping various combinations of toes. This is a simple and permanent marking method and does not appear to disturb the mice. These census checks upset the routine of the mice for one to several hours, but no adverse effect on litters or adults was noted. These are basically the same procedures used by Strecker and Emlen (1953).

The nests were classified as *platform,* if only a flat layer of nesting material existed; *bowl,* if a noticeable hollow was present; or *covered,* if the nest cavity was completely surrounded by nesting material. This follows the convention of Brown (1953). Nesting material in the form of shredded paper and cotton waste was added *ad lib.* for many months, until continued additions of material were not utilized by the animals. This generally occurred shortly after the populations attained maximum size.

A weighed amount of chicken mash (of composition given in Table I) was placed in each pen

TABLE I. *Food Composition*

Component	Percent by weight
Ground yellow corn	38.6%
Soybean oil meal	19.3
Wheat middlings	14.5
Wheat bran	9.6
Alfalfa wheatmeal	4.8
Meat scraps	4.8
Fortified dried whey	4.8
Oyster shells	1.4
Bonemeal	1.0
Iodized salt	0.5
Fish oil	0.5
Manganese sulfate	0.2

at two-, three-, or four-day intervals. The unused and spilled portions were swept up each time, weighed and the amount consumed was calculated.

Behavior observations were made from a high platform which provided a good view of all pens. Lights were turned on in the afternoon, so that the animals were little disturbed by the entrance and presence of the observer in the evening when the observations were made. For each pen, the number of fights or aggressive interactions, as described by Scott and Fredericson (1951), were recorded per unit of time.

From November, 1950, to December 26, 1951, the wooden barracks housing the population pens was heated during the cold months by an unjacketed coal furnace. This heating was inadequate and uncontrollable, and on December 26, a thermostatically controlled oil furnace was installed. The temperatures were then maintained at 68° to 70° Fahrenheit.

All animals dying in the course of the study were removed, and if they were sufficiently fresh, autopsies were done in an effort to determine the cause of death. At the termination of the study, all the mice were killed by ether and examined for reproductive condition.

Population Growth Forms

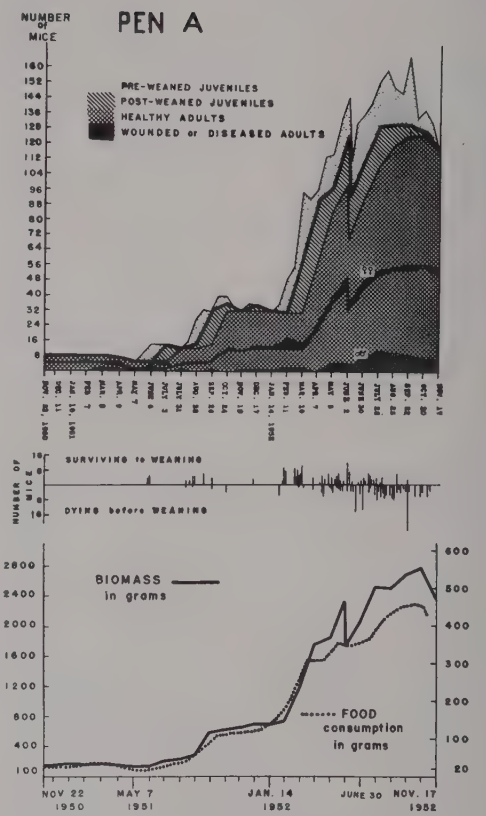
An outstanding characteristic of the population growth in the six pens was the variability exhibited in the rates of growth and in the numbers finally reached (Figs. 5-10).

The maximum number of postweaned mice attained in each pen was as follows:

Pen A—131	Pen C—127	Pen E—25
Pen B— 81	Pen D—138	Pen F—59

The concentrated pens (A, C and E) reached a mean level of 94 mice and the dispersed pens (B, D and F), a mean level of 93. This remarkable mean uniformity suggests that no over-all influence of habitat type prevailed, and the wide variation between pens of one habitat type (standard deviations of above means are 60 and 41 respectively) focuses attention on intrinsic factors within each population. The genetic and social backgrounds of the original mice of each population were apparently highly varied, and these backgrounds served as predominant population influences masking any effects the habitat differences may have produced.

In several cases the population exhibited S-shaped growth curves of various descriptions. In others, they reached a peak abruptly. The nature of the growth curve in any single population de-



FIGS. 5-10. Each figure portrays various aspects of the population in each pen. The graph at the top of the figure depicts the population growth in terms of numbers, sex, age and health composition.

The line chart in the middle of the figure shows the occurrence and survival of litters. The length of each vertical line represents the number of young born on any one day, and its position above or below the horizontal represents, respectively, survival or death. The time scale is the same as on the graph above.

The graph at the bottom of each figure shows the population growth in terms of total weight of weaned individuals (biomass) and food consumption. Figure 5 shows events in Pen A.

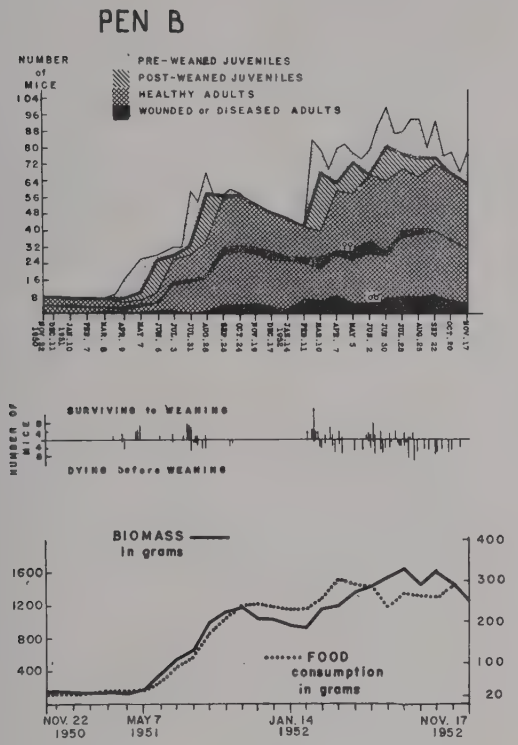


FIG. 6. Pen B.

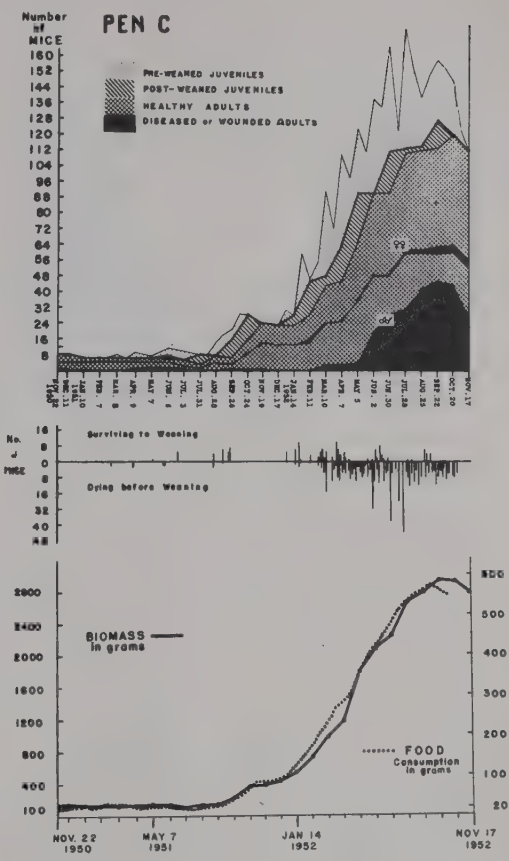


FIG. 7. Pen C.

pends upon the criterion of growth which is used; whether it is adult population, weaned population, total population or biomass. Generally, the curves of biomass provide the best S-shapes, whereas the population numbers display many erratic deviations (Figs. 5-10). It would be difficult, and perhaps misleading, to try to draw a single generalization concerning population growth forms which would apply to all six populations of this study.

Other studies of confined populations of house mice have also observed wide variation in population growth (Brown 1953; Strecker and Emlen 1953). Such variation might be expected from the observations of Crew and Mirskaia (1931). They studied the effects of density on individual house mice by confining adults in small cages and noted: "It was found that mouse differed from mouse temperamentally; some adapted themselves to the conditions of the experiment easily and quickly; others simply would not, or could not, do so. Some died or were killed shortly after their introduction; others exhibited a depressed sexual and reproductive activity, whilst others endured a very active sexual life but exhibited a low reproductive rate either for a time or else permanently."

A similar statement could be made about the populations of the present study. *Population* differed from *population* "temperamentally." Behavior observations described later in this paper reveal differences in the social behavior of the populations which apparently account for the variability in population growth.

Population Control

All six populations displayed two plateaus in their upward growth. The first occurred in the fall and winter of 1951-52; the second in the summer of 1952. These periods of population control revealed interesting differences in: (1) the demographic traits of natality and mortality resulting in population limitation, and (2) the circumstances, environmental and behavioral, which may have caused such limitation.

Winter 1951-52: a density-independent factor

Although the first period of population control in the six pens differed with respect to the time of inception, density level at inception, and duration,

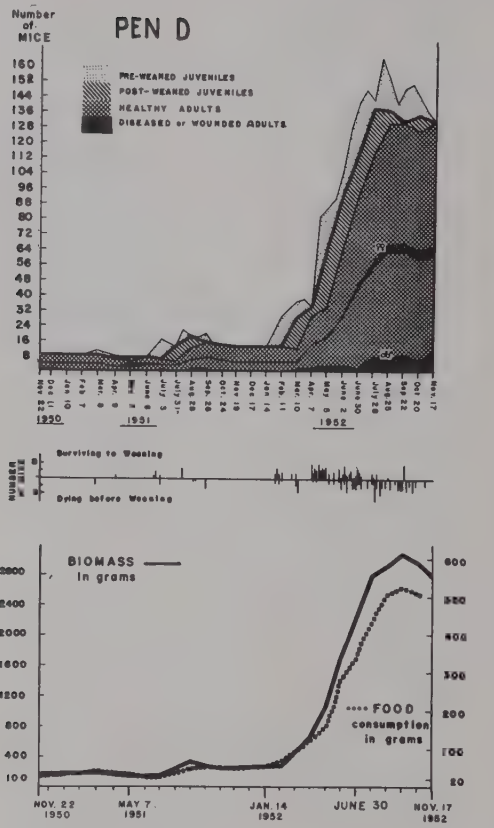


FIG. 8. Pen D.

it was characterized by reduced litter production (Figs. 5-10) and reduced pregnancy rates in every case. In November, December and the first half of January, only 20 young were born compared to 109 young born in the preceding late August, September and October. Concurrently, only 3 pregnancies were noted in November, December and January compared to 16 in the previous three months.

This decrease in litter production was apparently related to a reduction in fecundity.[2] On August 28, 1951, 77% of 52 adult females in all pens were perforate; on December 17, 1951, only 36% of 46 adult females were perforate. The adult males exhibited a similar decline in the percent that possessed scrotal testes. Although a perforate vagina and scrotal testes are crude measures of fecundity and have been criticized in pre-

[2] I shall use Park's terminology (in Allee, *et al.*, 1949, page 289): "Fecundity refers to egg production (or sperm production in males); fertility refers to the number of eggs that develop into living young."

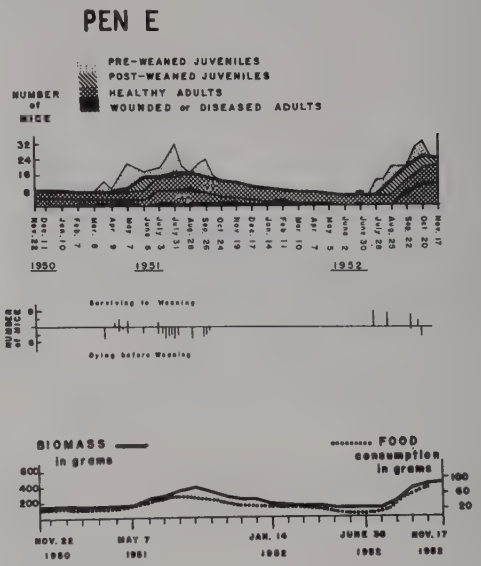


FIG. 9. Pen E.

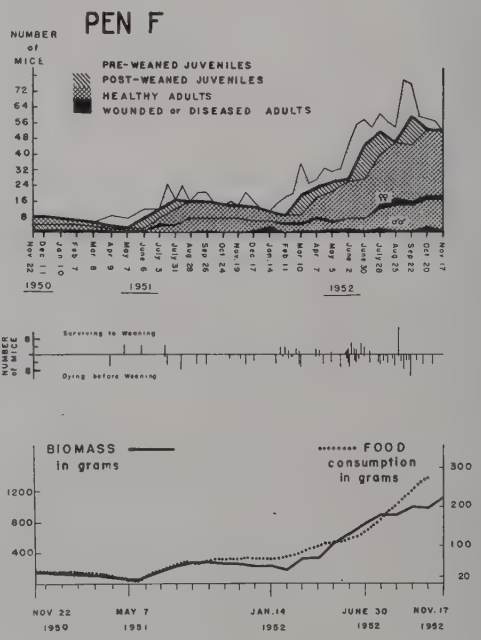


FIG. 10. Pen F.

vious studies (Laurie 1946; Jameson 1950), they offered some clues to reproductive condition in the live animal. At the termination of the study, the autopsy data revealed a surprisingly good correlation of these criteria with fecundity as determined internally (Table II).

TABLE II. *Autopsy Data on Reproductive Condition of Adults, November 17, 1952*

I. Males

Pen	Number of males	Testes socrotal	Testes 5 mm. or greater	Tubules of cauda epididymis visible
A.....	52	30 (58%)	24 (46%)	23 (44%)
B.....	31	24 (77%)	27 (87%)	27 (87%)
C.....	52	50 (96%)	50 (96%)	49 (94%)
D.....	61	34 (56%)	38 (62%)	33 (54%)
E.....	11	10 (91%)	10 (91%)	10 (91%)
F.....	17	15 (88%)	16 (94%)	15 (88%)

II. Females

Pen	Number of females	Vagina perforate	Uterus greater than 1 mm.	Visible corpora lutea
A.....	64	22 (34%)	33 (52%)	35 (55%)
B.....	31	20 (65%)	25 (81%)	23 (74%)
C.....	60	49 (82%)	51 (85%)	53 (88%)
D.....	70	38 (54%)	37 (53%)	44 (63%)
E.....	10	7 (70%)	3 (20%)	.....
F.....	35	25 (72%)	26 (74%)	11/15 (73%)

As possible factors causing this reduction of fecundity during the winter of 1951-52, food, cover, space, light, and temperature might be considered. The first two may be discarded at once since the mice were receiving an overabundance of both food and nesting material at all times, and in no cases were more than one-half the available nest boxes utilized.

Space does not seem to have been a limiting factor at this time since the populations subsequently all surpassed their 1951 levels. However, there is a possibility that a readjustment of behavior with respect to space requirements occurred in 1952 which effectively renewed population growth and permitted greater densities. If space was a limiting factor in the fall of 1951, it might help to explain why some populations ceased growth in August while others did not cease their growth until October (this will be considered in a subsequent section), but it would scarcely explain why all populations, at different densities, displayed reduced reproduction in the same winter months, October to February.

Although light has been shown to be a critical factor in the breeding of certain wild rodents (Baker and Ranson 1932), it is known that house mice may display high reproductive rates in greatly diminished daylight (Laurie 1946; Parkes 1924).

The major reason for the reduction in fecundity during the winter of 1951-52 would seem to be low temperatures. The heating system in the barracks was inadequate throughout the early winter, and between 4 and 6 hours of temperatures below 40° Fahrenheit would occur every night. This situation was corrected on December 26, 1951, by the installation of an oil furnace, and within a few weeks successful reproduction was resumed.

It is well established that house mice frequently fail to breed, or show depressed reproduction, in the winter (Baker 1946; King 1950; Parkes 1924; Southern and Laurie 1946; Strecker and Emlen 1953). Some house-mouse populations, however, may breed actively in winter; Laurie (1946) studying a sample of over 8000 house mice from three major habitats near Oxford, England, found the winter pregnancy rates to be as high as those of other seasons. Southern and Laurie (1946) observed high winter reproductive rates in house-mouse populations living in grain ricks, while house mice living in hedgerows and fields failed to breed in the winter. Apparently, natural populations of house mice can often maintain high rates of reproduction in spite of low environmental temperatures. On the other hand, populations living in artificial, seminatural, or unfavorable habitats frequently fail to breed in the cold of winter.

In summary, all populations displayed a plateau from October, 1951, to January, 1952. This period was characterized by lowered fecundity and decreased prevalence of pregnancy. Cold temperatures were the most likely cause, although in several pens the initial cessation of population growth occurred before the advent of cold temperatures. A survey of the literature suggests that cold is most effective in reducing reproduction when occurring in combination with other factors (Southern and Laurie 1946; Strecker and Emlen 1953).

Summer 1952: density-dependent factors

The second major period of population control occurred in the summer of 1952. Most of the populations attained their peak around mid-July and made no substantial increase in numbers thereafter. During this second period of population control, litter production did not decline markedly as it did in the first period. After July 14th, 710 young were born in 18 weeks, compared to 781 young born in the preceding 18 weeks. Quite clearly, failure to reproduce was not the major cause of population control.

Temperature, the most important factor governing population control in the winter of 1951-52, remained within limits favorable for the reproduction of house mice throughout the summer of 1952. Other physical factors were such as to favor successful reproduction. The most likely elements of control in the summer of 1952, there-

fore, would seem to be intrinsic or self-limiting factors.

Because of the independent and distinctive nature of population behavior in each of the six pens, the demographic characteristics of each population will be presented separately.

Case Histories of Individual Populations

Pen A

The population of Pen A increased rapidly throughout the spring of 1952 and reached a peak of 131 mice in late July and early August. It suffered an unfortunate accidental mortality of 32 adult and subadult mice on June 2, 1952, which temporarily altered the natural course of events in the population.[3] Apparently, the population of Pen A was near the crowding point when the accident occurred. Within two months the population had exceeded its former level, but shortly thereafter it ceased to grow.

The most obvious mechanism which limited the population was the failure of litters to survive (Fig. 5). Nestling survival fell from 97% of 62 young in February and March, 1952, to 14% of 99 young in August and September.

Although nestling survival was the primary trait controlling the population, other demographic changes occurred to influence population control, particularly in its latter stages. Birth rates declined gradually in July and August to low levels in October and November (Fig. 12). Pregnancy rates followed a similar pattern of decline. Fecundity fell markedly in October and November (Fig. 12). At autopsy in November, only 55% of the females had visible corpora lutea and only 44% of the males had visible tubules in the cauda epididymis (Table II).[4] The possible significance and explanation of these changes will be discussed after all six populations are considered.

The mortality rates of postweaned mice showed rather consistent patterns in the six populations, and will be discussed collectively in a later section.

Pen B

Pen B reached its maximum number of 81 weaned mice on June 30, 1952. Littering continued as frequently after the peak as before (Fig. 6). There was an obvious failure of litters to survive after the population peak, however. Nestling survival fell from 77% of 44 young in February and March to 13% of 60 young in August and September. Thus the major mechanism of population limitation in Pen B was the same as in Pen A.

Other reproductive characteristics, however, which accompanied continued population control were different in Pen B than in Pen A. There was no major drop in birth rates, pregnancy rates, or fecundity percentages in Pen B throughout the fall of 1952, whereas all three traits declined in Pen A (Fig. 12).

Pen C

Pen C attained its maximum number of 127 weaned mice on September 22, 1952. The immediate causation of abrupt population limitation was again failure of litters to survive. Of 63 young born after the population peak, none survived.

Birth rates also played a fundamental role in population limitation in Pen C, for they exhibited a marked decline throughout the summer and fall of 1952 (Fig. 12). Pregnancy rates declined throughout the same period.

There was not, however, a corresponding fall in fecundity (Fig. 12). The final autopsies showed that 94% of the males were still producing sperm, and 88% of the females possessed corpora lutea. Pen C therefore represents a paradoxical situation: declining birth and pregnancy rates, but no decline in fecundity. A possible explanation of this will be offered in a later section on fertility.

Not only was the relative fecundity of Pen C higher in November than either Pen A or Pen B, but it had consistently been higher throughout the preceding summer and fall. Customarily, 95% of the females in Pen C were perforate at each census compared to only about 80% in Pens A and B, and the same relationship held for the percentage of males that were scrotal. Thus the populations revealed basically different fecundity ratios.

The high fecundity and productivity in Pen C did not produce a larger populaton than Pen A. Although more young were born in Pen C, more died, to make the net population increment approximately equal to that in Pen A.

Fighting was unusually prevalent in Pen C throughout the summer and fall of 1952. It caused few deaths directly, but led to wounding, scabbiness, and mite infestations (*Bdellonyssus bacoti* Fonseca) —conditions which may have increased mortality of postweaned subadult mice in the fall (Table III). Although both sexes were observed to fight, apparently the males fought oftener and with greater severity, for only males developed open wounds. Figure 11 shows the typical poor condition of 75% of the males in Pen C during the fall of 1952 (the incidence of this condition among the males of any other population did not exceed 12%). It is of particular interest that this scabbiness was nonexistent in the

[3] During the census checks, corks were customarily placed in the holes of the nest boxes to confine the mice until they could be handled. In two boxes, which happened to contain 19 and 20 mice on June 2, 1952, the mice succumbed to heat exhaustion before the effects of this confinement were discovered. Thirty-two mice died. The day was unusually hot, and coupled with the crowding of the mice, the temperature in the boxes rose to over 100° Fahrenheit. It is to be emphasized that the mice were not forced into the boxes; they occurred there of their own inclination, but once the corks were placed in the holes, the mice were excited and their ventilation was reduced. They had been confined less than 30 minutes when the mortality was discovered. Several of the animals were alive when removed, but died within two hours.

[4] These characteristics are frequently chosen as good indicators of fecundity (Laurie 1946; Jameson 1950; Linsdale and Tevis 1952; Strecker and Emlen 1953).

TABLE III. *Mortality Rates of Postweaned Mice*

	Before population peaks (Apr.-May-June)			During population peaks (July-August)			After population peaks (Sept.-Oct.-Nov.)		
Age Class:*=	I	II	III	I	II	III	I	II	III
Pen									
A	4/97 (4%)	1/140 (1%)	6/106 (6%)	4/41 (10%)	2/108 (2%)	6/92 (7%)	5/20 (25%)	4/126 (3%)	15/244 (6%)
B	9/47 (19%)	0/87 (0%)	14/137 (10%)	5/24 (21%)	5/74 (7%)	12/60 (20%)	2/12 (12%)	0/112 (0%)	14/93 (15%)
C	1/46 (2%)	0/138 (0%)	2/107 (2%)	0/24 (0%)	0/104 (0%)	2/96 (2%)	5/16 (31%)	1/102 (1%)	10/243 (4%)
D	0/79 (0%)	0/92 (0%)	0/48 (0%)	4/46 (9%)	2/149 (1%)	3/58 (5%)	3/16 (19%)	3/212 (1%)	9/174 (5%)
E	0/0	0/0	2/25 (8%)	0/0	0/0	0/10 (0%)	1/21 (5%)	0/22 (0%)	4/15 (27%)
F	0/21 (0%)	0/45 (0%)	3/29 (10%)	0/30 (0%)	4/44 (9%)	2/23 (9%)	4/14 (29%)	0/66 (0%)	4/78 (5%)

*Age Classes I - post weaned, subadults, 3 weeks to 6 weeks in age.
II - prime adults, 6 weeks to 6 months in age.
III - adults over 6 months in age.

FIG. 11. Typical scabby adult male in Pen C. Scabbiness was initiated by fighting and intensified by feeding activity of mites.

females of Pen C although they were living in the same mite-infested nest boxes. I conclude that fighting and wounding were necessary antecedents in producing this acarine dermatitis. Apparently, the open wounds on the males attracted the mites and provided a point of entrance. The fighting may also have reduced mutual grooming and thus enhanced the prevalence of the mites. Calhoun (1949) has observed that fighting wounds on Norway rats may serve as egg-laying sites for flies.

Pen D

Pen D abruptly reached its maximum number of 138 weaned mice on July 28, 1952, and thereafter declined gradually. Cessation of population growth was again due primarily to high nestling mortality. Nestling survival declined from 91% of 65 young in April and May to 12% of 65 young in August and September.

The birth rates declined throughout the period of population control and were accompanied by a similar decline in observed pregnancies (Fig. 13).

The population of Pen D also exhibited a declining fecundity from September to November, and thus resembled Pen A in all major demographic aspects (Fig. 13).

Pen E

The population of Pen E, which never grew above 25 mice over a two-year period, provided one of the most unusual and interesting histories of the study. For an understanding of events in the pen, it is necessary to return to its beginnings in the spring and summer of 1951.

At an early date, Pen E showed promise of developing a large and productive population. On June 6, 1951, it had attained a population of 15 weaned mice compared to only 5 in Pen A and 7 in Pen C. However, the population failed to increase as expected, and of 50 young which were born after June 6, only 2 survived to weaning. Excessive litter mortality was again the major factor limiting population growth. Laboratory cultures from freshly dead nestlings revealed no evidence of pathogens which could explain the mortality.

The behavior observations indicated that the population of Pen E was undergoing a period of internal strife, which was later found to be characteristic of the other populations as they were intrinsically controlled by crowding at higher population levels. This internal strife consisted of intense aggressive activity, breakdown of female nest defense,

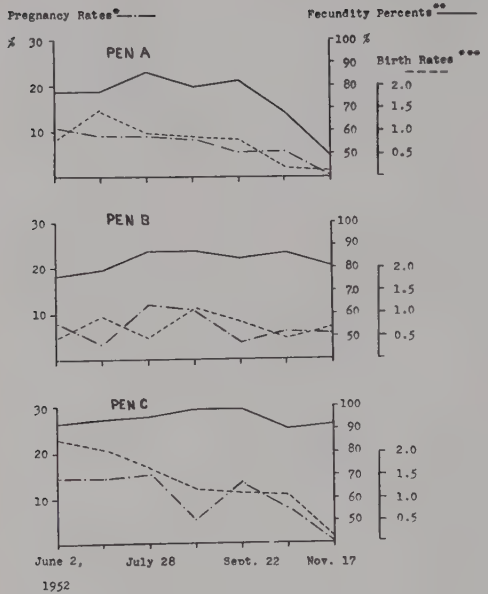


FIG. 12. Pens A, B, and C.

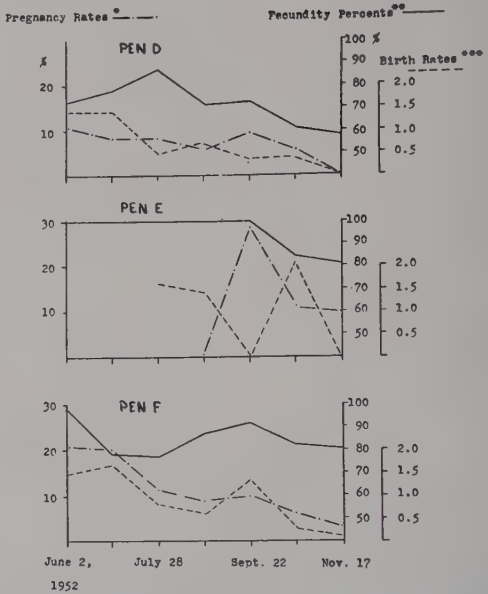


FIG. 13. Pens D, E, and F.

FIGS. 12-13. Relationships between fecundity, pregnancy rates and observed birth rates of mature populations.

* Pregnancy rate—number of adult females pregnant at each census divided by number of adult females present.

** Fecundity percent—average of adult male and adult female fecundity; determined by external criteria from June through October, and by internal criteria in November.

*** Birth rate—number of young born per adult female per four-week period.

disruption of female nest building, and general social instability leading to cannibalism and litter desertion. I conclude that these behavioral traits were related to crowding and confinement, but not to density *per se*, for the population of Pen E was "crowded" at a density of one mouse per 10 square feet, whereas the populations of other pens were not "crowded" until they reached densities 10 times greater.

Throughout the fall and winter of 1951-52, the population of Pen E declined. More males died than females, so that by February only 1 male and 7 females remained. No pregnancies occurred, however, and the one male died in May of 1952. Thus this pen, which had showed early potentialities of growth, declined and suffered self-extinction.

In late June, a young male was introduced for three weeks into Pen E to determine if the surviving females were capable of bearing young. Subsequently, several litters were born. Apparently the previous failure of successful reproduction in the pen was associated directly or indirectly with the former males.

Pen F

The population of Pen F attained an initial peak of 52 weaned mice on July 28, but two months later it reached a second peak of 59 weaned mice. Again the major factor of population limitation was low survival of litters, not a complete lack of litters being born (Fig. 10).

Pen F also follows the pattern of Pens A, C and D by displaying falling birth rates and pregnancy rates. In terms of fecundity, however, there was not a prominent drop (Fig. 13).

Pen F possessed an average litter size of 4.2 young per litter for 59 litters born throughout the two years. This is significantly smaller than the average litter size of 5.1 young for 356 litters in all other pens.[5] The population of Pen F was characterized by considerable inbreeding,[6] plus the possible presence of recessive lethal genes.[7] Such a combination might help to explain the reduced litter size.

[5] *t*-value for means is 3.071. Probability of this occurring by chance is less than 0.01.

[6] In the early history of Pen F, natural mortality reduced the population to one pair of adults from which the subsequent population developed.

[7] Five males from Pen F were sent to Dr. L. C. Dunn of Columbia University for genetic testing of the t-locus. Although none of these five males contained lethal t-alleles, subsequent testing of males wild-trapped from the same source as the Pen F mice revealed one male in a sample of 12 which contained a t-allele. For information on the mode of action of t-alleles see Chesley and Dunn (1936), and for their occurrence in wild house-mouse populations, Dunn and Morgan (1953).

Discussion of Demographic Factors

Litter Mortality

The major mechanism of population control in each pen was a high litter mortality, apparently related to population pressure. None of the pens was actually limited by a failure of litters to appear.

Much of this litter mortality was due to direct cannibalism and some of it was apparently due to desertion and improper parental care. Some dead young were found partly consumed, while others appeared intact or possessed only surface wounds. Frequently, the dead nestlings were strewn about the floor of the pen, and the mortality could have resulted from a variety of causes including being bitten, deserted, or suffering general rough treatment. It was impossible to make rigid distinctions between cannibalism and other forms of improper parental care as the cause of death. Demographically, these behavioral traits were similar and together they formed the major mechanism of population control in response to crowding.

Several behavioral circumstances which apparently fostered cannibalism and litter desertion were: (1) intense aggressive activity within the population, (2) breakdown of normal female nest defense, (3) encroachment of many adults upon the nest site, and (4) destruction of the nest. Data on these behavioral traits will be presented in a subsequent paper.

Other studies have also found improper parental care to be important components of population control. Brown (1953) observed litter mortality to be the most important factor controlling the upper limit of his experimental populations of house mice. He concluded that successful weaning of litters completely ceased in populations when the number of mice increased to the level at which their activities caused all parturient females to eat their young. In Brown's study apparently all cannibalism was attributable to adult females, but in my populations both males and females were observed in the act of eating young.

Crew and Mirskaia (1931) noted that litters of house mice were often eaten by adults under conditions of high density, but they provided no details. Chitty (1952), in a study of natural vole populations, noted that strife during the breeding season resulted in early death of the young and physiological derangements among the adults. This intraspecific strife according to Chitty, was a major form of population control, and probably had competition for space at its roots.

These studies and many others (Allee *et al.* 1949; Boyce 1946; Calhoun 1949; Crombie 1946; Errington 1939; Solomon 1949; etc.) indicate that cannibalism and similar forms of intraspecific strife are frequently major aspects of population control in response to crowding in a wide variety of organisms.

Birth Rate

In all pens except B and E, the period of population control after June and July, 1952, was characterized by gradually declining birth rates (Figs. 12 and 13). The relatively stable birth rates in Pen B were probably associated with the more uniform growth and early attainment of maturity in this population. Pen B suffered no violent fluctuations and no periods of acute crises, while Pens A, C, D and F all attained their peaks in a short time, and by their rapid growth apparently precipitated acute population crises. Pen E represented a very small population of special circumstances (see former section on Pen E).

Thus, Pen B was the only pen controlled solely by increased mortality rates. This may be, however, a common pattern of population control among moderately stable rodent populations (Davis 1953).

Prevalence of Pregnancy

In all of the populations that showed declining birth rates after the population peaks (A, C, D and F), the pregnancy rates also declined (Figs. 12 and 13). In June and July, 1952, an average of 12% of all adult females in these pens were pregnant at each census; in August and September, this average had fallen to 8%; and in October and November, to 3.5%. Pens B and E, however, revealed pregnancy rates of 6% to 11% in October and November, and indicated that an over-all environmental influence was not responsible for reducing the prevalence in the other pens.

Since the pregnancy rates declined concurrently with the birth rates and in similar magnitude, it is not likely that foetal resorption was a factor causing the reduced birth rates. Furthermore, no cases of foetal resorption were found in the autopsy of 270 females in November. Although we cannot completely dismiss the possibility of early embryonic resorption, it seems most likely that the declining pregnancy rates were due to diminished conception rates.

Fecundity

Pens A and D exhibited a declining fecundity which paralleled the decline in birth rates (Figs. 12 and 13). Pens B, C and F, however, did not display this fall in fecundity, although, as already noted, Pens C and F exhibited falling birth rates and pregnancy rates. These variations in repro-

ductive characteristics are of particular interest in view of the essentially uniform physical environment in the pens. We are faced with several different facts to explain. Why did the fecundity fall in Pens A and D, and not in Pens C and F? Why did the birth rates decline in Pens C and F when the animals still remained fecund?

Previous population studies have domonstrated a decrease in fecundity with crowding in both vertebrate and invertebrate animals (Allee *et al.* 1949; Birch, Park and Frank 1951; Frank 1952; Pearl 1932; etc.). In most of these studies, the authors attributed the harmful effects of crowding to both physiological and psychological disturbances. The explanation of Pearl (1932) is typical: "The individual female does not lay as many eggs when under crowded conditions; first, because she is directly interfered with in the act of ovipositing; secondly, because she is undernourished, her normal feeding being continually interfered with; and thirdly, because she is continuously excited and fatigued."

Other investigators singled out food as the most importanct factor determinig fecunity. Kluijver (1951) observed a declining fecundity during high density in great tit (*Parus major*) populations, and Lack (1952) attributed this to lowered food supply. Johnson (1933) presented evidence that density effects in *Oxytricha* are largely dependent upon the ratios of *Oxytricha* and its bacterial food supply. Robertson and Sang (1944) reached a similar conclusion that crowding reduces fecundity in *Drosophila* only when food is short. Sang (1950) reiterated this viewpoint when he wrote: . . . "Crowding *per se* has no effect on fecundity nor has competition between females at the oviposition surface. . . . Restriction of the food supply, on the other hand, has a notable effect, and this suggests that crowding influences fecundity only indirectly by regulating the amount of food available to each female."

Food consumption records in the mouse populations of this study suggest a similar relationship. In three populations (B, C and F) which maintained high food consumption—3.7 to 4.5 grams per mouse per day—from June to October, the fecundity remained high despite severe crowding. In two populations (A and D) which displayed low food consumption—3.1 to 3.4 grams per mouse per day—from June to October, the fecundity declined (Table IV). These results are in close agreement with those of Strecker and Emlen (1953) which showed that the fecundity of a population of house mice was greatly reduced when the food consumption approached or fell below 3 grams per mouse per day.

TABLE IV. *Data on Food Consumption and Fecundity*

Pen	Food Consumption*		Fecundity percentages‡
	Grams per mouse mouse**	Grams per gram of mouse* of mouse†	
A.....	3.1	.16	50
B.....	3.7	.18	80
C.....	4.5	.20	91
D.....	3.4	.16	58
E.....	2.2	.11	..§
F.....	3.7	.19	80

*Average consumption per day from June to October 18.

‡*F*-value on the differences of these averages is 44.75. That necessary for significance at the 1% level is 3.70. Hence a highly significant difference is present.

†*F*-value on these averages is 13.75. That necessary for significance at the 1% level is 3.70.

‡These fecundity percentages represent the average of the fecundity percentages for both sexes as determined by autopsy on November 17.

§This percentage is omitted because corpora lutea counts were not made on the females; the other criteria of fecundity which were used differ widely on the females of this particular pen (See Table II).

Since a surplus of food was constantly available in all of the pens, the explanation for this differential food consumption between various populations would seem to lie in some behavioral factor affecting food consumption or food requirements. The records of Pens A, C and D are particularly interesting in this regard. My behavior observations indicated that several despotic mice in Pens A and D prevented subordinate mice from feeding freely. These highly dominant individuals were antagonistic toward each other, and in Pen A they would often feed at separate times, so that at least one despot was at the feeding area throughout much of the day and the night. In Pen D the despots occupied and dominated different regions of the pens. It is conceivable, but still quite hypothetical, that such a societal structure would have reduced the food consumption of the subordinate mice which comprised the major portions of the populations. The subject merits further study and must be evaluated from the viewpoint of feeding rhythms, recognition of dominant mice by subordinate mice, and weight records of dominant mice compared to subordinate mice.

Pen C was characterized by more aggressiveness and fighting than Pens A or D. This intense fighting, apparently resulting from a very unstable society in which no mice had a clear-cut dominance, may have made possible greater food consumption by the individual mice, or it may have made greater food consumption necessary. Unfortunately, the data of this study can do little to elucidate these interesting problems.

Fertility

Pens C and F displayed a declining prevalence of pregnancy throughout their periods of popula-

tion control in spite of the fact that they maintained high fecundity. Pen C provided the most striking example. The prevalence of pregnancy in Pen C fell from 13% during the four months preceding August 1, to 7% during the succeeding four months. The number of young born concurrently declined from 331 to 187, and the specific birth rate fell from 1.79 to 0.81 young per adult female per month. Yet in November just as many females were ovulating and just as many males showed evidence of sperm production as in April, May, June and July.

An explanation is suggested by concurrent observations on copulatory behavior in the pens. As the population of Pen C became crowded, prolonged copulations by one male on a female were less frequent. Many mice, apparently males, would gather around a copulating pair, and several males would attempt to mount at once. Usually the male astride a female would be knocked off. No one male could remain astride a female for more than a second or two. This was in striking contrast to the more normal copulation times of 5 to 10 seconds prevailing in Pens A, B and D.

Calhoun (1949) found that in rat populations in which the males were not organized into a stable social order, groups of males would follow an estrous female and repeatedly and briefly mount. These females showed a very low rate of conception, possibly because no single male was able to complete the copulatory act (Scott and Fredericson, 1951). Calhoun used the term "copulation pressure" to describe this phenomenon and believed that it may be an important mechanism of population control in dense populations. Southern (1948) has noted the disruption of copulation in the European rabbit (*Oryctolagus cuniculus*) and suggested that a high density would cause interferences with mating activities by other members of the colony. Fulton (in Collias 1944) observed that if pigeons are crowded in pens, the males continually interfere with each other's attempts at copulation, and the fertility is greatly reduced. Armstrong (1942) has cited other references among birds showing that coition in the open stimulates interference from other members of the same species. Among many natural aggregations of vertebrates, territorialism and dominance hierarchies apparently function to prevent this type of interference.

It seems likely that excessive "copulation pressure" was present in Pens C and F and may have been responsible for the decline in fertility in these pens. Other possibilities exist, however, (*e.g.*, failures in early embryonic development) and the subject of fertility changes in populations merits further attention.

Mortality of Postweaned Mice

Although the mortality of postweaned individuals was not a major mechanism of population control, a marked increase in the death rates of subadults occurred in Pens A, C, D and F after the population peaks (Table III). The populations in these four pens reached their peaks abruptly and apparently precipitated some social change which increased the subadult mortality rates. This increase in subadult mortality rates did not occur in Pen B, most likely because Pen B reached its population peak early and suffered no violent fluctuations or periods of acute crises. Its demographic features remained moderately stable as did its population level. Pen E possessed no subadults in the spring and summer, and in the fall only 1 out of 21 subadults died.

In Pens B and F, slight increases in the mortality rates of prime adults occurred during the population peaks, but these increased rates did not prevail after the peaks (Table III, Fig. 14).

The mortality rates of adults over 6 months of age remained basically unchanged before, during and after the population peaks (Fig. 14).

Throughout all periods of population growth and control, the mortality rates of prime adults were lower than those of subadults and adults over 6 months of age (Fig. 14). A similar mortality pattern has been described for several species of mammals (Calhoun 1949; Evans and Holdenreid 1943; Hamilton 1941; Murie 1944; Linsdale and Tevis 1952).

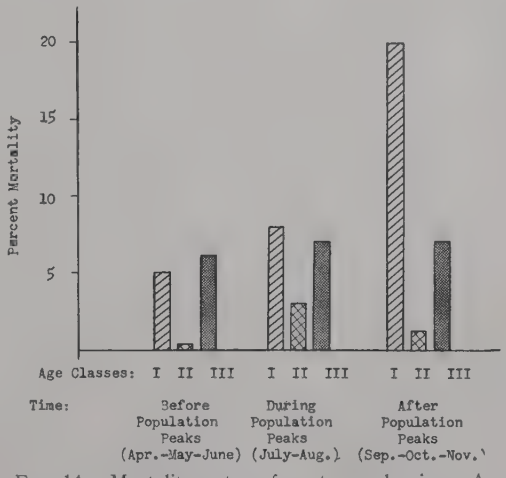


FIG. 14. Mortality rates of postweaned mice. Age classes: I—postweaned, subadults, 3 to 6 weeks in age; II—prime adults, 6 weeks to 6 months in age; III—adults over 6 months in age.

Autopsies performed on 55 mice from all pens dying of natural causes throughout the two years suggested the following causes of death: unknown, 25; fighting, 6; infectious arthritis, 5; nephritis, 4; pneumonia, 4; typhoid, 4; staphylococcal abscesses, 2; carcinomas, 2; apparent senility, 2; infectious catarrh, 1. The autopsies consisted of gross examination of the viscera, and the pathological symptoms used for diagnosis were those given by Dingle (in Snell 1941) and Twort and Twort (1932). Since most dead mice were found several hours after death, it was not feasible to obtain culture material from them, and the above diagnoses, based on gross pathology alone, must be regarded with some reservation.

Summary

This paper presents demographic and behavioral data on the growth, maturation and limitation of six confined populations of house mice. The study was designed to provide: (1) specific information on natural controlling mechanisms of mouse populations which were given constant surpluses of food, and (2) general information on mammalian population dynamics, with particular attention to crowding phenomena.

Each population lived in a pen 6 by 25 feet supplied with 48 nest boxes and a continuous surplus of food, water and nesting material. In three of the pens the food and housing facilities were spaced throughout the pen, and in the other three pens these facilities were crowded at opposite ends.

Each population was started with four pairs of wild-trapped house mice, and was permitted to develop naturally until several months after growth had ceased. Nest boxes were examined for nestlings every two weeks and every four weeks all mice were caught, weighed, examined and then released in the pen.

Population growth varied widely between pens, some populations attaining a level of over 130 adult mice while one did not grow above 25 mice during a two-year period. This variability in growth was not related to the physical environment, but was usually attributable to behavioral traits and social structure.

There was no noticeable effect due to concentrated housing and feeding facilities compared to dispersed facilities. Differences in the behavior and productivity of the mice themselves were apparently more important.

In the first winter, all populations exhibited temporary plateaus during which reproduction ceased. This was correlated with and apparently caused by cold temperatures.

In the second summer, all populations ceased growth as a result of social disturbances related to crowding. Reproductive activity did not cease; rather, the major mechanism of population limitation was excessive litter mortality due to cannibalism and desertion.

Reproductive responses to crowding varied greatly among the six populations. Birth rates continued unchanged in one population, and none of the basic reproductive traits other than litter survival was adversely affected by crowding in this pen.

In four populations, birth rates gradually declined with continued crowding. In two of these populations, the declining birth rates were apparently due to a declining fecundity of the mice; that is, fewer males were producing sperm and fewer females were ovulating. This was associated with a reduction in food consumption per mouse which occurred despite an abundance of food. Several highly dominant mice in these two populations apparently prevented subordinate mice from feeding freely.

In the other two populations, food consumption did not decline and fecundity remained high. The declining birth rates in these populations were possibly due to excessive copulation pressure (that is, the constant interference of normal copulation due to the presence of many males), or to failures in early embryonic development. These populations had a very unstable social structure in which no individuals were noticeably dominant.

Although the mortality of postweaned mice was not an important mechanism of population control, the mortality rates of postweaned subadults increased significantly after the populations had reached their peaks, while the mortality rates of adults were largely unaffected.

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RELATIONSHIP BETWEEN GRASS DENSITY AND BRUSH SEEDLING SURVIVAL[1]

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Introduction

In many California foothill range lands, brush seedlings emerge in large numbers nearly every year, but most of them are dead by the end of the first summer. After brush fires, seedlings emerge in even larger numbers, and, ordinarily, conditions for growth and survival are excellent, so that the resulting brush population may be far more dense than that of the original stand. In the former instance, herbaceous vegetation shades the brush seedlings and uses soil moisture; but, in the latter case, light and soil moisture supply are ample for optimum brush seedling development.

Reseeding to forage plants following controlled burning of brush is now extensively practiced in the foothills of the California coast ranges and the Sierra Nevada. Such reseeding is done with four principal objectives: (1) to provide forage for game and livestock, (2) to provide a plant cover to lessen soil erosion, (3) to furnish competition to reduce survival of brush seedlings, and (4) to supply fuel for a reburn to further reduce the brush cover if necessary (Schultz and Biswell 1952). This study is concerned with the third objective, that of providing competition for the brush seedlings.

Description of Study Area

Vegetation

The study was made in woodland-grass vegetation at elevations between 1,000 and 3,500 feet on the western slope of the Sierra Nevada in Madera County, central California. Characteristically, the vegetation consists of annual grassland with scattered blue oak (*Quercus douglasii* H. & A.), interior live oak (*Q. wislizenii* A. DC.), and digger pine (*Pinus sabiniana* Dougl.) trees. Several species of nonsprouting shrubs, notably wedgeleaf ceanothus (*Ceanothus cuneatus* (Hook.) Nutt.), chaparral whitethorn (*C. leucodermis* Greene), and Mariposa manzanita (*Arctostaphylos mariposa* Dudley), occur in varying abundance, depending upon the past history and management of the area (Fig. 1). A few sprouting shrubs occur also, such as yerba santa (*Eriodictyon californicum* (H. & A.) Torr.) and redberry (*Rhamnus crocea* var. *ilicifolia* (Kell.) Green).

Fig. 1. Woodland-grass vegetation on the west slope of the central Sierra Nevada foothills, Madera County, California, elevation 1,100 feet. Trees and shrubs include blue oak, interior live oak, digger pine, wedgeleaf ceanothus, and Mariposa manzanita. Grassy foreground is comprised of predominantly annual species.

Where shrubs occur as isolated plants, they are surrounded by stands of annual grasses and forbs of high densities except directly under the crowns of the shrubs. The chief grasses are soft chess (*Bromus mollis* L.), foxtail fescue (*Festuca megalura* Nutt.), red brome (*B. rubens* L.), slender oats (*Avena barbata* Brot.), and ripgut grass (*Bromus rigidus* Roth.). Common forbs are broadleaf and red-stem filaree (*Erodium botrys* Bertol., *E. cicutarium* L'Her.), annual clovers (*Trifolium* spp.), and Spanish clover (*Lotus americanus* (Nutt.) Bisch.). Frequently, however, especially at the higher elevations, the shrubs occur as dense brushfields, several to many acres in extent. Here the soil surface is mostly shaded and is nearly devoid of herbaceous vegetation (Fig. 2).

Climate

Mean annual precipitation varies from 18 inches at 1,000 feet elevation to about 32 inches at 3,500 feet, but during the years of the study it was about three inches higher than average. Nearly all of the rain comes during the months of October through May. Snow seldom falls, but frequently the temperature at the soil surface drops below freezing during the winter.

[1] Contribution from cooperative investigation between the University of California and the California Department of Fish and Game. Work was done under Federal Aid in Wildlife Restoration Act, Pittman-Robertson Research Project 31-R entitled "Effects of Brush Removal on Game Range in California."

FIG. 2. A full density stand composed of whitethorn chaparral at about 2,000 feet elevation in Madera County. The ground under the brush is bare of herbaceous vegetation.

Soils

Plots and excavations were confined to soils of two series: Coarsegold and Holland. Both are residual soils derived from igneous rocks. The Coarsegold soil is a reddish brown, fine, sandy loam in the first 6 inches, and grades through very fine, sandy loam, loam, and clay loam or clay in successive 10-inch intervals. The structure is lumpy throughout and the pH ranges from 6.0 at the top to neutral at the lowest horizon. At 4 to 5 feet, the soil grades into fragmented schist with dark red clay in fissures.

The Holland soil is grayish brown in color and is a sandy loam throughout. The top 8 inches have a fair amount of organic material. This soil frequently has a depth of 5 feet or more.

In Madera County, there are about 350 square miles of upland soils at the elevations to which the study was confined. About 45 square miles are of the Coarsegold Series and 305 are of the Holland. The two series extend both northward and southward from the county.

Management practices

The shrub cover in a given area to be controlled-burned is never uniform in density nor homogeneous in species. Where scattered shrubs occur in a matrix of grass, spots of heavy white ash, no larger in diameter than the crowns of the woody plants, are found as islands in the black ashes of the grass fire. Grass fires are not exceptionally intense so that many seeds of the annual species remain unharmed, far more than are necessary to insure establishment of another good herbaceous cover.

Where dense brushfields are burned, a rather uniform bed of heavy white ash is found over the entire area, and there are fewer seeds of resident herbaceous species.

Areas of heavy ash on controlled burns are generally reseeded before the fall rains to various grasses and legumes, either singly or in mixtures. Both annuals and perennials are used for reseeding, depending on the site and the principal objective of future management. Annuals commonly used are domestic ryegrass (*Lolium multiflorum* Lam.), cereal rye (*Secale cereale* L.), and rose clover (*Trifolium hirtum* All.). More recently, soft chess, one of the resident annuals, has been used. The recommended and commonly used perennials include hardinggrass (*Phalaris tuberosa* var. *stenoptera* (Hack.) Hitch.), smilo (*Oryzopsis miliacea* (L.) Benth. and Hook. ex Aschers. and Schweinf.), and tall fescue (*Festuca arundinacea* Schreb.). Figure 3 shows a portion of an area which had been controlled-burned. The left hand side was reseeded to domestic ryegrass; the right hand side was not seeded.

FIG. 3. This area had formerly been dense brush. It was controlled burned and portions reseeded to domestic ryegrass. The left hand side shows a stand of mature ryegrass, the unseeded right hand side, a dense population of one-year-old wedgeleaf ceanothus, chaparral whitethorn, and yerba santa seedlings.

EFFECT OF GRASS DENSITY ON SURVIVAL AND VIGOR OF BRUSH SEEDLINGS

There is a direct correlation between the amount of herbaceous vegetation, especially grasses, and the number and vigor of brush seedlings when the two kinds of plants are growing together. In the present study, the production of herbaceous vegetation was measured in terms of foliar density. Weight of tops would be a more accurate measure of production but also more difficult to obtain. Counts were made to ascertain brush seedling survival while height measurments were considered an estimate of their vigor.

The characteristic relationship between the density of herbaceous vegetation and brush seedling numbers continues from the time of emergence of the brush seedlings through the time of maturation of the herbaceous plants. Both the number and the vigor of the brush seedlings are adversely affected by increasing densities of grasses and forbs.

The manner in which numbers are affected by different densities of grass cover can be shown by use of regression lines. Studies of this kind were made in the north coast region of California, in Lake County, where the brush seedlings were primarily chamise (*Adenostema fasciculatum* H. and A.), and the grass was chiefly domestic ryegrass (Biswell, *et al.* 1952). Where the grass density was in the neighborhood of 5 per cent or less, there were over 200 chamise seedlings per milacre remaining after the grass had dried in summer. But where the density was around 25 per cent, there were less than 30 seedlings remaining per milacre. Hedrick (1951) found that the regression of chamise seedling numbers on grass density was linear between the 5 and 55 per cent density classes, but, at very low or exceptionally high densities, no correlation could be established.

In the present study, there were indications that some of the brush species are better able to survive in high densities of grass than others. A detailed investigation of this observation is now underway. Also, it was observed that more brush seedlings survived in stands of some species of grasses than in others, even when these occurred at equal densities. This, too, is being investigated with the use of a large number of forage plants. The present study considers the influence of two artificially seeded species, domestic ryegrass and hardinggrass, and of resident annuals collectively on the survival of brush seedlings. In addition, ryegrass was manipulated by denuding and clipping.

Ryegrass

One study area consisted of 15 acres in the center of a large brushfield which was nearly an impenetrable stand of wedgeleaf ceanothus, chaparral whitethorn, deerbrush (*Ceanothus integerrimus* H. and A.), and Mariposa manzanita. The area had been burned in August, 1950. Over the 15-acre area all nonsprouting brush plants were killed by the fire, and many of the stems, especially those of wedgeleaf ceanothus, were consumed. A thick layer of white ash was present and formed an ideal seedbed for grass. Three 5-acre divisions were made, and in October, 1950, these were seeded by hand to 5, 10, and 15 pounds of domestic ryegrass per acre. Abundant winter rains resulted in a uniform, dense stand of ryegrass.

Six hundred one-square-foot plots were used to sample this study area in April and again in August, 1951. These were placed at random, irrespective of rates of seeding. For each plot, the foliar density of the vegetation, which was mostly ryegrass, was estimated in one per cent intervals up to 5 per cent and above this, in 5 per cent intervals. The living brush seedlings were counted.

Curvilinear regression lines were calculated from the data (Fig. 4). The upper, broken line represents the number of brush seedlings in April. Where there was no grass in the proximity of the brush seedlings, there were, on the average, 7.8 seedlings per square foot. Based on the slope of the curve, it would have taken a grass density of at least 85 per cent to eliminate brush seedlings entirely. In annual vegetation, of course, such coverage is seldom obtained as early as April. The average grass density based on all plots was 18 per cent, and there were 3.8 seedlings per square foot over the 15-acre area, or 165,000 per acre.

The lower, solid line of Figure 4 represents a count of the living brush seedlings in August after the ryegrass had dried. At zero grass density, there were now 2.8 seedlings per square foot. At this time, a grass density of 55 per cent was sufficient to reduce brush seedlings to zero. For the 15-acre area, the average density of grass was 32 per cent, and there was .8 brush seedling per

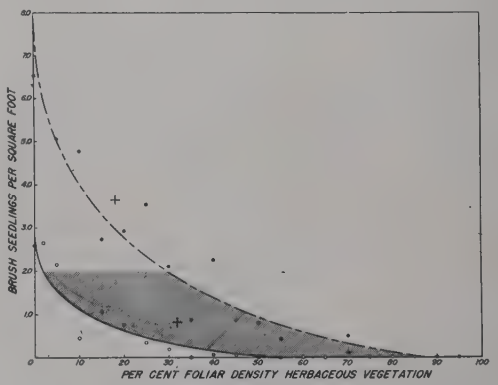

FIG. 4. Regression of numbers of brush seedlings per square foot on foliar density of herbaceous vegetation where ryegrass was seeded. Broken line: April sampling; solid line: August sampling. Dots and circles are means for grass density classes for April and August, respectively. Shaded portion represents brush seedling mortality between April and August which can be attributed directly to competition from the ryegrass. Crosses are sample means.

square foot or 35,000 per acre. Whereas in April there were no plots with 85 per cent density, which was then needed to reduce brush seedlings to zero, in August one third of the plots exceeded the 55 per cent density which was needed to choke out all seedlings.

A 64 per cent mortality of brush seedlings took place in plots which contained no herbaceous vegetation. Perhaps more significant, however, is the fact that the number of seedlings in these plots was reduced to an average of 2.8 per square foot. This and other sampling through the study area indicate that no matter how dense the original population of brush seedlings, about two per square foot survive the first growing season when no other competing vegetation is present. Percent mortality, therefore, is more nearly determined by the original number of seedlings than by the final number.

Additional mortality—beyond two per square foot—is almost entirely attributable to ryegrass competition within the plots. This is shown by the shaded portion of Figure 4. It may be seen that above 30 per cent grass density all the mortality is due to ryegrass competition. As the grass density decreases below 30 per cent, an increasing proportion of the mortality is attributable to intraspecific competition and other causes.

Several characteristics of the data are not shown in Figure 4. One is a skewed distribution of plots in density classes, the 5 per cent class being best represented, followed by 3, 0, 10, 15, and so on in approximate numerical order. The other is that the standard errors of density class means are much higher at 0 and 3 per cent and beyond 55 per cent. That is to say, many microareas of a square foot or more in size may support no brush seedlings because the soil may be too thin, seed may have washed away, or some other disturbance may have occurred. For the same reasons, there may be no grass on these spots. On the other hand, on plots where no grass seed happens to have fallen, there may be as many as 20 healthy brush seedlings. This explains the high variability in seedling numbers in the very low density classes. There are relatively few plots in each interval between 55 and 100 per cent; consequently, when one or several plots contain one or two seedlings, however low in vigor, the data appear to have great variability.

The slope of the curves might be slightly different if the plot size were larger than one square foot. It is inconceivable that ryegrass plants just outside the borders of the plot would have no effect on the brush seedlings within the plot, since the root systems of either have a radius of more than 12 inches. But for the purpose of comparing a sampling in spring with one in summer, or comparing the effect of one grass species with another, the factor of plot size would seem to have little importance.

Hardinggrass

Another 15-acre study area also sampled with 600 one-square-foot plots in April and August, 1951, gave similar information for hardinggrass. The brush was mashed with a bulldozer about 6 months before it was burned in August, 1950. In all other respects, the area was similar to the one already described. The area was seeded to hardinggrass at the rate of 4 pounds per acre. An excellent stand was obtained. Scattered patches of native grass occurred where few hardinggrass plants became established. Plots falling in native annual vegetation were not considered in the sample.

Curvilinear regression lines plotted from these data are shown in Figure 5. The upper, broken line, or April count, shows fewer brush seedlings than were present in the area seeded to ryegrass. This may be accounted for by several factors: greater intensity of fire, few or no 1950 seed produced as the brush had been broken down before flower formation, or different edaphic and microclimatic conditions. An average of 3.3 seedlings per square foot were found where there was no hardinggrass or other herbaceous vegetation in the plots. Some seedlings remained until a density of 80 per cent hardinggrass was attained, but this density was reached on only one of 600 plots. The average density for the area was 16 per cent.

By August (lower, solid line, Fig. 5), two seedlings remained at zero density, and seedling survival was zero at 45 per cent density. Meanwhile, total density for the area had increased by only 6 per cent.

The shaded portion of Figure 5 represents the proportion of the brush seedling mortality attributable to competition from the hardinggrass growing within the plots. The proportionately smaller unshaded area between the curves compared to that in Figure 4 is due to the sparse April population of brush seedlings in the hardinggrass, and not necessarily to greater competitive capacity of the hardinggrass.

Resident annuals

Although fires in dense stands of brush may be intense, there are usually some seeds of resident annuals present which escape injury. These, plus seeds transported onto the burned areas, germinate readily and often make up a sparse cover when domestic species are not sown. These annuals may occupy spaces missed in broadcast

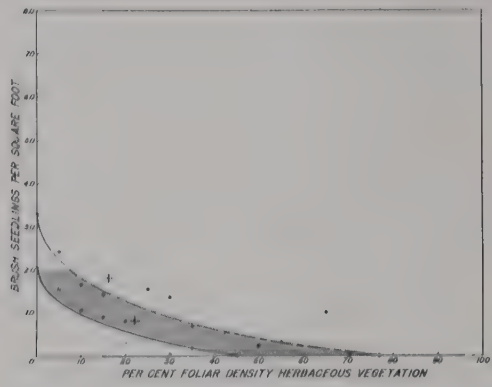

FIG. 5. Regression of numbers of brush seedlings per square foot on foliar density of herbaceous vegetation where hardinggrass was seeded. Original brush seedling population was not as high as in the ryegrass plots.

seeding. They are largely absent where artificially seeded stands are dense. Therefore, a typical burned area reseeded, for example, to ryegrass contains patches bare of any grassy cover, small areas of sparse resident annuals, and a matrix of ryegrass growing in nearly a pure stand.

A reseeded area such as that described above was sampled with 500 one-square-foot plots in the summer of 1952, the measurements taken being foliar density of all herbaceous vegetation to the nearest 5 per cent and number of brush seedlings per plot. The sample was separated into those plots containing ryegrass only and to those containing resident annuals only; the same zero density plots were used for both groups. Regression lines were drawn from the data to show the relationship between grass density and brush seedling numbers (Figs. 6, 7). Linear regression was used because the calculations are not as time-consuming as in computing curvilinear regression.

Where there was no grass, an average of 2.3 brush seedlings occurred per square foot. Where the herbaceous cover was domestic ryegrass only, the regression line crossed the zero brush seedling line at 39 per cent density (Fig. 6). Density of 39 per cent was exceeded in 15 per cent of the total of ryegrass-only and no-grass plots sampled. Where the herbaceous cover consisted only of resident annuals, the zero brush seedling line was crossed at 66 per cent density (Fig. 7). The highest density sampled was 60 per cent, obtained only twice in 210 plots; this is 6 per cent less than that required to choke out all seedlings. The average density was only 6 per cent. The average number of brush seedlings was 2.2 per square foot, equivalent to 96,000 per acre. Even if a uniform maximum density of 60 per cent were attained there would still be .2 seedlings per square foot or 8,700 per acre.

Manipulated grass cover

An area of approximately two acres was selected from a controlled burn of 1951 in which domestic ryegrass was the most important reseeded species. The area had a nearly uniform cover of brush ash after the burn and many brush seedlings germinated during the spring of 1952.

Three milacre plots were located at random in each of ten places. On one plot the herbaceous vegetation was removed, on the second plot the herbaceous vegetation was clipped to one-half inch each week, and on the third the vegetation was left undisturbed. Each treatment had ten replications. Clippings were made weekly until August 13, when growth ceased. Denuding was done on April 16 by removing all vegetation except the brush seedlings and any subsequent growth was kept out.

Seedling numbers and average heights were recorded every two weeks. The stages of development of the herbaceous vegetation and seedlings were also noted.

Foliar density measurements, using 100 points, were taken in each plot at the peak of the rye-

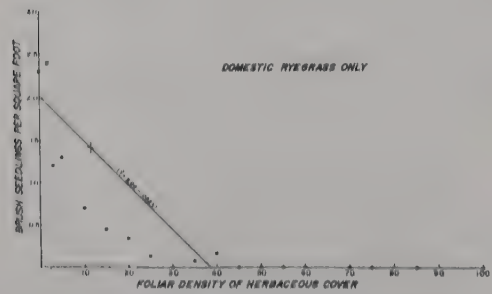

FIG. 6. Regression of numbers of brush seedlings per square foot on density of ryegrass in August after the ryegrass had matured.

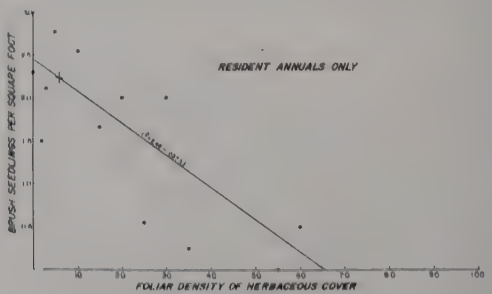

FIG. 7. Regression of brush seedling numbers on density of resident annual vegetation, predominantly grasses, in August after the grass had matured.

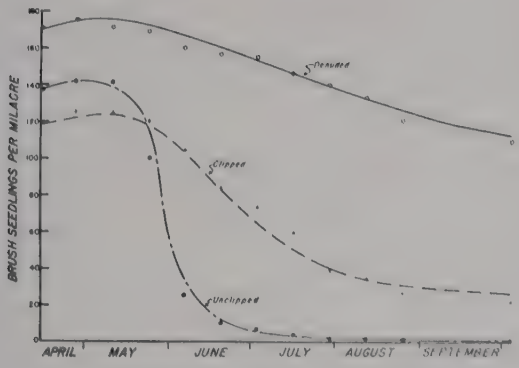

FIG. 8. Mortality of brush seedlings shown by numbers of live seedlings in plots where herbaceous vegetation was removed, clipped weekly, and left unclipped. Average herbaceous density at maturity in these plots was 0, 10, and 50 per cent, respectively.

grass growth. In the unclipped plots the average herbaceous density was 50 per cent; in the clipped plots, 10 per cent.

The number of brush seedlings alive at the end of each two-week period is shown in Figure 8. There was some variation in the numbers of seedlings in each treatment at the start of the study. Some germination took place in each treatment until April 28.

There was a gradual death loss of brush seedlings in the denuded plots throughout the study. A more pronounced death loss, however, occurred among the seedlings in the clipped plots. The mortality rate was gradual and did not show any period of rapid loss such as in the unclipped plots where most of the seedlings died between May 8 and June 18.

In terms of numbers per acre, the data show that on October 3 there were approximately 108,000, 27,000, and 1,000 seedlings in the denuded, clipped, and unclipped plots, respectively.

Average heights of seedlings indicate that clipping the grass had a pronounced effect on their growth increment (Fig. 9). The rate of growth was nearly the same in each treatment until the middle of May, after which the seedlings in the denuded plots grew rapidly, those in the clipped plots grew slowly, and those in the unclipped plots ceased growth about June 4.

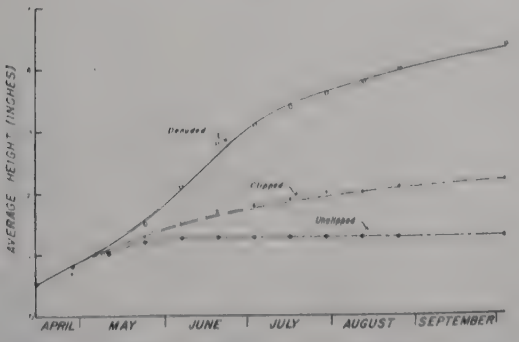

FIG. 9. Average height of brush seedlings in plots where herbaceous vegetation was removed, clipped weekly, and left unclipped.

Seedlings in the denuded plots appeared vigorous and healthy throughout the season; while those in the other two treatments appeared wilted after about the first of June and remained so until it rained in the fall.

EMERGENCE AND DEVELOPMENT OF SEEDLINGS

Emergence and growth of grass

Seedlings on controlled burns are made prior to the fall rains. Ryegrass and resident annuals usually emerge between one and six weeks after the first heavy rain; while hardinggrass does not emerge until three to 11 weeks after rain. The exact length of time depends partly on the depth of ash, the type of soil, and the weather, especially day and night temperatures (Juhren, *et al.* 1953). It was found that about two inches of rain are necessary to initiate germination in heavy brush ash.

After emergence, growth of the grass is more or less sporadic but generally slow, because the weather is constantly getting colder and the number of sunny days less frequent. Frequently, leaf growth during the months of December, January, and February may be stopped entirely for several consecutive weeks when the night temperatures dip below 32° F., and the days are cold and cloudy. Root growth, however, may not be as severely retarded during this winter period. Excavations of ryegrass roots in December 1950, and January and March, 1951, showed continuous growth in depth while little or no foliage growth was taking place. In mid-January, ryegrass had roots extending to an average of 8 inches; in early March, to 12 inches. In March, the seedlings were still in the 2- and 3-tiller stage as they had been in January while less than one-half inch had been added to the average leaf length. Some of the resident annual grasses were similar to ryegrass in this regard, except that depth of roots in January and March averaged 6 and 8.5 inches, respectively.

Growth accelerates when warmer and drier weather begins. This period of rapid growth for annual vegetation extends for about six weeks, between March 1 and April 15. The beginning of this period corresponds with the time of maximum emergence of the brush seedlings. Most of the tillering and leaf development and much of the root growth of the annual grasses occur during this time. By mid-April of 1951, near the end

of the period of rapid growth, most of the ryegrass tillers had been produced and roots had penetrated to 23 inches. This is a late-growing species. Sixty-eight, 74, and 83 per cent of the height growth of the resident annuals—soft chess, foxtail fescue, and broadleaf filaree, respectively —was made during this period of rapid growth (Talbot and Biswell 1942). A far lesser proportion of one year's growth is made by the perennial grasses during this period.

Drying of the annual forage begins in late April and continues during May. During this period many green plants may dry completely in a few days of hot weather. Ryegrass matures and dries more quickly the taller and denser the stand. Under close grazing it may remain green until August. A large proportion of the root development takes place at the time when the soil is low in available water and the foliage is beginning to dry. Ryegrass roots excavated in July, when the plants were completely dry, had extended to 56 inches. This represents about three additional feet in depth since the period of rapid top growth. Reseeded perennials such as hardinggrass frequently remain green all summer. If, however, they grow in dense stands or on sites which are extremely dry, dormancy and rapid drying may ensue during July or August.

Emergence and growth of brush seedlings

Wedgeleaf ceanothus, chaparral whitethorn, Mariposa manzanita, and yerba santa are the most important brush species in the study areas. Emergence of seedlings of these species begins around the middle of March and is about 80 per cent complete by the middle of April (Fig. 10), with some variation from year to year.

Chaparral whitethorn is the first to emerge. During 1951, two-thirds of all the seedlings of this species appeared in the week of March 14 to 21. Two-thirds of the wedgeleaf ceanothus seedlings emerged between March 14 and March 28. Manzanita seedlings reached their peak of emergence one week after chaparral whitethorn and yerba santa two weeks after that. The behavior in emergence was similar for all species in that each reached its peak in numbers soon after germination began, and thereafter seedlings appeared infrequently and sporadically. This behavior seemed to be correlated with the weather. Late February and the first two weeks of March were cool and cloudy; the weather warmed after March 14 and maximum germination took place. A shower of about 2 inches came during the last week of April. This resulted in further germination.

Similarly, in 1952 whitethorn chaparral was earlier to emerge than wedgeleaf ceanothus. On

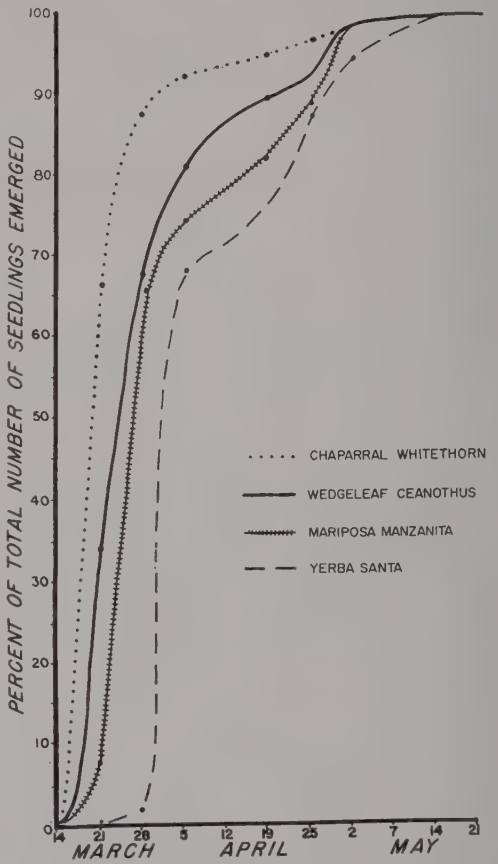

FIG. 10. Per cent of total numbers of brush seedlings of four species which emerged in the spring of 1951. Seedling counts were made at weekly intervals.

southern exposures, the peak of emergence for the former species was prior to March 13; while the peak for wedgeleaf ceanothus was near March 20. On north-facing slopes the peaks for the same species were April 3 and April 10, respectively.

The increase in size of the brush seedlings after emergence is steady and rapid when growing at some distance from other plants. Under such conditions growth continues unchecked throughout the summer. Seedlings of chaparral whitethorn are frequently 2 or 3 inches tall within a month after emergence, 7 to 8 inches in three months, 12 to 13 inches in five months, and 18 to 20 inches in nine months (by December). Wedgeleaf ceanothus does not grow as rapidly in height, but branches and expands laterally to a greater extent than chaparral whitethorn. Nevertheless, seedlings of this species attain heights of 2 inches in a month, 4 to 5 inches in three months, and 8 inches in nine months. Root systems of both species can

extend to 5 or 6 inches two weeks after germination, and 14 to 15 inches in a month, and 3 to 4.5 feet within three months.

Seedlings of Mariposa manzanita may attain heights of 4 to 6 inches during the first season; while yerba santa may attain a height of 20 inches.

Root Studies

Cooper (1922) states that one of the most important features of the chaparral is the root system, which is extensive in proportion to the size of the plant. Further, Cannon (1911) said that some of the roots are deeply penetrating, but the major part of the root system is superficial. Neither Cannon nor Cooper intimate the depths which may be attained except to say that the neighborhood of the water-table may be reached. Cannon states that the deeper roots are the first to develop, while the superficial ones are formed later in the life of the plant.

Root systems of a number of chaparral species were excavated during the first year of seedling development. Wedgeleaf ceanothus seedlings, about 15 days after emergence, had tap roots averaging 4.5 inches in length. In two more weeks they had more than doubled their depth of penetration. In three months (by the first week in July) roots had reached depths of 30 to 43 inches (Fig. 11). Roots of chaparral whitethorn seedlings averaged 25 per cent shorter than those of wedgeleaf ceanothus. The excavations were made in Holland and Coarsegold sandy loam soils between 5 and 6 feet deep.

The roots illustrated in Figure 11 were from seedlings growing without competition from any plants other than members of their own species. The seedlings were robust, but not the largest available. Roots of other seedlings were excavated which were growing in a dense stand of ryegrass. The tap roots of 3-month-old wedge-

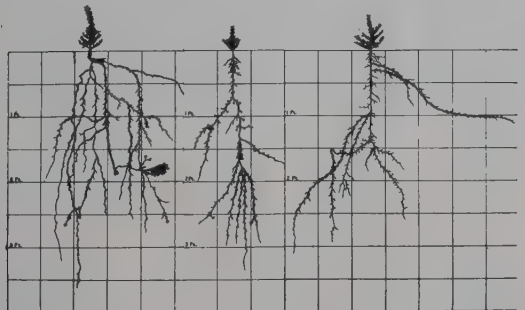

Fig. 11. Sketches of root systems of three-month-old wedgeleaf ceanothus seedlings excavated from Coarsegold sandy loam. There was no herbaceous vegetation in the vicinity. Greatest depth of penetration was 43 inches on July 4; greatest lateral growth, 26 inches. Tops were 6 to 8 inches tall.

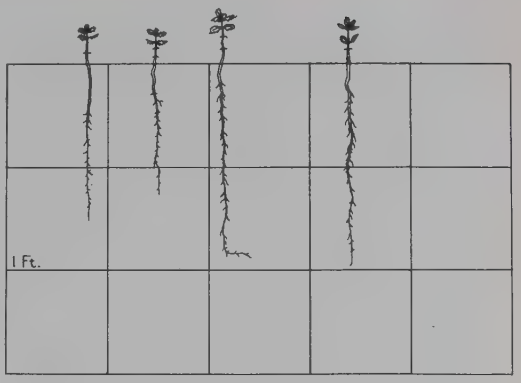

Fig. 12. Sketches of four 3-month-old wedgeleaf ceanothus root-systems taken from a spot about 5 yards distant from those in Figure 11. This spot had been seeded to ryegrass, which attained a foliar density of 70 per cent at maturity. Deepest penetration was 11.5 inches; there was very little lateral development. Tops were about 2 inches tall.

leaf ceanothus seedlings attained a maximum depth of 11.5 inches under such conditions and exhibited very little branching (Fig. 12). Roots of chaparral whitethorn seedlings of the same age were similar in appearance.

By way of contrast with the brush seedling roots, the fibrous grass roots occupy the soil much more completely. Of the two grasses most frequently mentioned in this study, ryegrass has roots which are finely branched and in contact with a large proportion of the soil particles; while the hardinggrass roots are much coarser (Fig. 13). Ryegrass roots weighed 2.3 times as much as hardinggrass roots from an equal volume of soil, taken from the level 6 to 12 inches below the crown of plants of the two species. The tops of the ryegrass and hardinggrass plants from which the roots were taken were about equal in size.

Soil Moisture Relationships

Two series of investigations were made to relate competition between grass and brush seedlings to soil moisture; one in depth and the other through time. The studies were made in the Coarsegold soils. Roots of both grass and brush species penetrate easily in this soil when moisture for growth is available.

First, two excavations were made: one in an ungrazed ryegrass plot, where the herbaceous density was about 70 per cent; and another about five yards distant, in an unseeded plot which had no vegetation except brush seedlings. The excavations were made during July, 1950. The ryegrass had matured by that date.

In the ryegrass plot, nearly all of the brush seedlings had died by the time the grass was completely dry. These seedlings had grown only

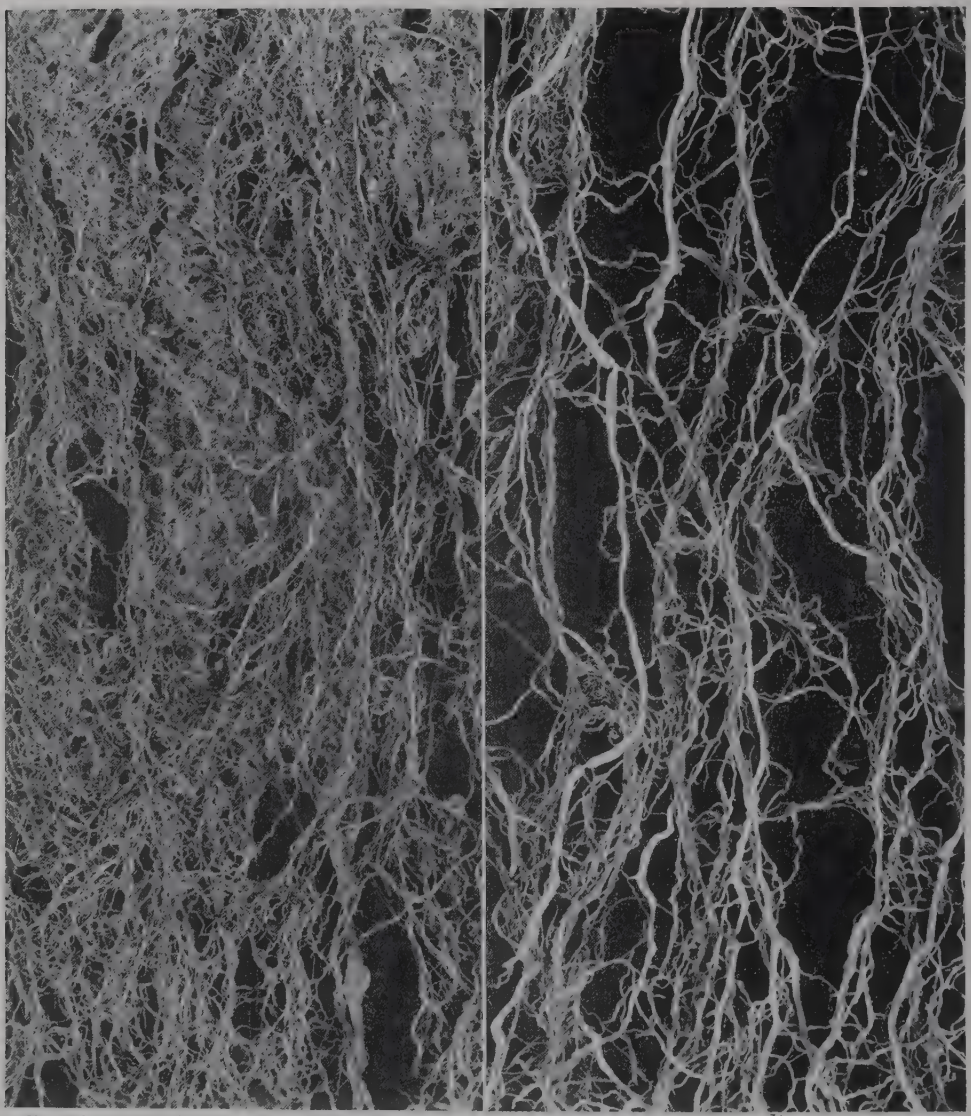

FIG. 13. Roots of grasses taken from blocks of sod 4 inches thick, and at the depth of 6 to 12 inches below the crowns of the plants. Ryegrass on the left, hardinggrass on the right. Roots are shown life size. Roots of the ryegrass were 2.3 times heavier than those of the hardinggrass.

2 inches tall (Fig. 12). The brush roots had penetrated a maximum of only 11 inches. The ryegrass roots had penetrated over 4.5 feet. The soil moisture deficiency zone for plants, as determined by the wilting point for sunflowers, extended down more than four feet. These relationships are shown diagrammatically in Figure 14.

In the unseeded plots, the brush seedlings were vigorous and averaged 8 inches in height. Few, if any, had died from drought. Their roots extended to a maximum depth of 43 inches (Fig. 11). The soil moisture deficiency zone extended down only 6 inches (Fig. 15).

The second investigation consisted of making soil moisture determinations from May through September in the denuded, clipped, and unclipped plots described previously.

Soil moisture samples collected weekly at one-foot intervals down to 4 feet indicated that considerable differences existed in the amount of

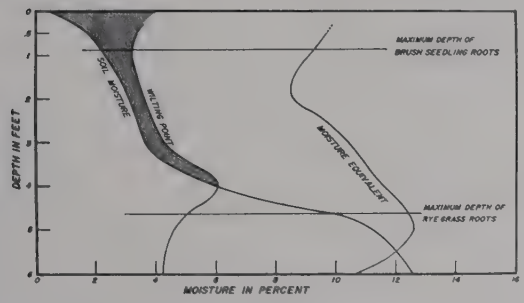

FIG. 14. Soil moisture in relation to depth of rooting of ryegrass and brush seedlings in Coarsegold sandy loam. Shaded portion represents soil moisture deficiency for sunflowers. Soil moisture samples were taken and root excavations made on July 4, 1950, after the ryegrass had matured. Foliar density of ryegrass was 70 per cent; roots in Figure 12 taken from this spot.

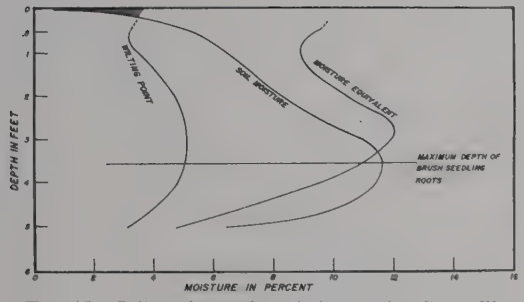

FIG. 15. Soil moisture in relation to brush seedling roots where no herbaceaus vegetation was present. Roots in Figure 11 taken from this spot.

moisture lost in each treatment (Table I). After the last rains in April, there was approximately 13.5 per cent soil moisture. The vegetation in the undisturbed plots used most of the available water in the upper foot of soil within a month from that time. Figures 16 and 17 which have been plotted for the first and second foot of soil indicate that the wilting point was reached in the first foot near May 12, June 10 and July 10 in the unclipped, clipped and denuded plots, respectively. During May, the brush seedlings in all treatments were still less than one and one-half inches in height, and most of their root systems were confined to the first foot of soil. In the unclipped plots, apparently, the wilting point was reached in the first foot early enough to cause the high mortality of brush seedlings during May and June. In the denuded and clipped plots, however, the brush seedling roots penetrated below the one-foot level before the moisture reached the wilting point. Wilting point determinations indicate that the soil moisture became unavailable only in the upper foot of soil.

The amounts of soil moisture in the third foot of the clipped and the denuded plots were about

TABLE I. *Average per cent soil moisture based on dry weight of soil under three treatments. Soil moisture samples were taken in six milacre plots in each treatment*

Treatment	Depth	Date (1952)									
		5/20	5/27	6/3	6/10	6/17	6/24	7/1	7/16	7/29	8/12	9/22
Denuded	1st foot	9.2	8.0	8.2	7.4	6.7	6.0	5.6	4.8	3.7	3.4	3.4
	2nd foot	12.2	10.7	10.8	10.8	10.4	9.8	9.3	9.0	8.7	8.0	8.1
	3rd foot	13.0	12.0	12.2	12.1	11.9	10.8	10.7	10.9	10.4	9.8	9.9
	4th foot	12.6	12.9	12.5	12.9	12.3	11.9	11.6	11.8	10.4	10.2	10.1
Clipped	1st foot	7.4	5.8	5.5	4.6	4.4	4.2	3.8	3.7	2.9	2.7	2.6
	2nd foot	10.5	9.6	10.0	8.7	8.2	8.2	9.3	8.4	6.8	7.4	7.5
	3rd foot	12.6	12.9	12.1	12.4	10.7	11.6	11.5	10.5	10.0	9.2	8.9
	4th foot	13.5	13.5	12.7	12.8	11.7	12.0	12.4	11.5	10.6	10.6	10.2
Unclipped	1st foot	3.8	3.0	3.6	3.0	3.2	2.9	2.8	2.6	2.4	2.5	2.4
	2nd foot	7.3	6.6	7.0	6.2	6.8	6.3	6.2	6.4	5.5	5.9	5.9
	3rd foot	11.4	10.5	10.1	9.5	10.4	9.0	9.2	8.7	8.4	9.0	8.9
	4th foot	13.5	12.6	11.4	11.8	11.8	10.8	11.1	10.7	10.8	10.5	10.7

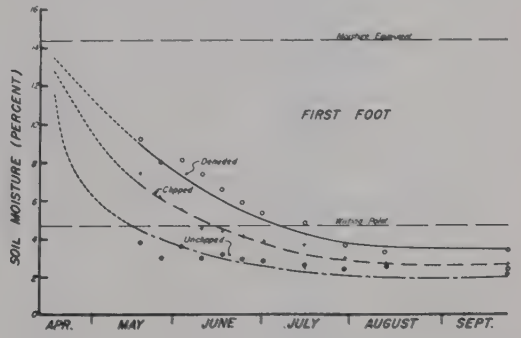

FIG. 16. Average per cent soil moisture in the first foot of soil in plots in which the herbaceous vegetation was removed, clipped weekly, and left unclipped. Data from first, fifth, and ninth rows of Table I.

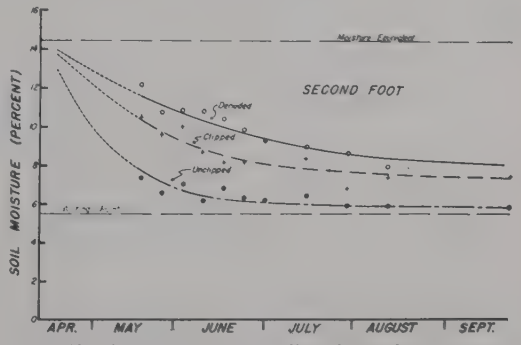

FIG. 17. Average per cent soil moisture in the second foot of soil. Data from second, sixth, and tenth rows of Table I.

equal. The third foot of the unclipped plots showed more moisture loss through the season, indicating that the herbaceous vegetation was using moisture at that depth. In the fourth foot, all measurements and treatments showed about the same soil moisture content.

The data presented in Figures 14 and 15 show similar relationships except that the soil moisture deficiency under grass extended to a greater depth.

Discussion

The data presented have both ecological and agronomic implications. Plant succession and competition, when understood well enough so that they can be regulated and controlled, can be tools for wise management of forage and browse in brush covered areas.

Plant succession and competition

In woodland-grass vegetation, the tendency is towards increase in woody plants (Biswell 1954). The increase is not so much invasion of new territory as a thickening of stand in the vicinity of parent plants. The three non-sprouting species of shrubs, wedgeleaf ceanothus, chaparral whitethorn, and Marpiosa manzanita all produce seeds in great quantity. Proportionately few seeds, but numerically many, germinate every year. Ordinarily, most of the seedlings die. Mortality may be caused by drought and use of moisture by other plants, browsing and trampling, insects, or disease. But, after a fire, more seeds germinate and a higher proportion of the seedlings survive. Thus, brush burned either by wildfires or by controlled fires, or even when cleared by mechanical means, will revert to a stand of brush of greater density unless some control of this plant succession is operative. Plant competition affords one control measure. In competition, the advantage lies with those plants, individuals as well as species, that are first present. The term "competition" is here meant to include any or all limiting effects plants may have on each other, directly or indirectly through the environment such as toxic substances exuded from the seedlings, light, nutrients, soil moisture, space, or other factors.

Herbaceous species which seed naturally or grasses which are seeded on burned brushlands germinate and emerge in the fall, while the brush seedlings do not emerge until the following spring.

The basal area of the grasses is high by the time brush seedlings emerge. It is impossible for a seedling to emerge where a plant already occurs. This may be construed as competition for space. More accurately, the hypocotyl cannot push through the roots and stem bases of the grass.

The foliar density of the grasses is high when the brush seedlings emerge, and many of the latter come up under the dense shade of grass foliage. Observations indicate that mortality of these seedlings is high during the late spring months.

The grasses have well-established, fine, fibrous root systems which more thoroughly occupy the soil than do the tap roots of the young brush seedlings. The grasses use more water than the young brush seedlings, and soil moisture is exhausted before brush roots get very deep. Only in years of exceptionally late spring rains would the grass not deplete the soil moisture beyond the needs of the developing brush seedling.

If a positive correlation can be assumed between grass density above ground and the occupancy of the soil by grass roots, then grass density is a good measure of plant competition for soil moisture. That brush seedling mortality is correlated with grass density in the same way would indicate that this mortality is chiefly a matter of competition for soil moisture. Inferences drawn from the clipping experiment corroborate such a conclusion.

The grasses may excrete an inhibitor to germination or early development of the brush seedlings as does mustard (Went, *et al.* 1952). No attempt was made to study this but the possibility is recognized. However, if such an inhibitor exists, it is of little importance during the latter half of the growing season. Competition for nutrients, light, or space evidently contributes to the mortality of seedlings up to time of moisture depletion below the wilting point.

The availability of soil moisture is the most striking factor influencing seedling survival.

Brush control and range management

From the standpoint of a brush control program, the principles involved in this study are applicable only the first year after burning or clearing. If the brush seedlings are not controlled during the first growing season they may grow below the maximum penetration of grass roots the following spring so that moisture will be available to them in subsequent years. Other control measures would then be necessary, such as chemical sprays, reburning, or grazing management. Since seedlings germinate in greatest abundance the first year after fire, it follows that the greatest benefits can be obtained by seeding to control this initial brush seedling crop. Moreover, stands of grass are more easily established in the ash seedbed of a recent fire than on an area burned a year or more previously.

Not only does a dense cover of grass reflect a high degree of competition for the young brush plants, but it also indicates good ground cover to prevent soil erosion and high production of forage. It behooves the range manager to use a high-yielding and fast-growing species and to seed uniformly and at optimum rates (Schultz and Biswell 1952). In management for deer, where browse is needed, a scattered population of brush

FIG. 18. Diagram showing the relationships between grass density and brush seedling survival. Explanations are contained in the summary. Drawing scaled in accordance with actual data presented in the text.

seedlings is desirable. The heterogeneity of soil and sites on brushy ranges is usually such that uniformity of grass cover is never attained; therefore, unless the practice of reseeding is supplemented by reburning or spraying, excellent deer range results.

The study indicates two methods of grazing management for cattle where annual grass and brush seedlings are growing together. Grazing may be deferred until the grass has matured. At this time the brush seedling is still green and is browsed readily, as there are few other green plants available. Commencing grazing early in winter or spring prevents the maintenance of maximum transpiring surface. It does, however, promote tillering and prolongs the transpiration of water. In the process of grazing, many brush seedlings are eaten or pulled out of the ground. Thus, full use is made of the grass as forage, without appreciably reducing the effect of competition.

The principles involved in this relationship between grass density and brush seedling survival are applicable generally in regions of Mediterranean climate. The principal qualifications are a brush seed population which responds to clearing practices, a lag in time of emergence of brush seedlings after herbaceous vegetation, and the cessation of rain early in spring before the brush roots penetrate to the same depth as do the grass roots. The intensity of the relationship is modified by soil type and depth, and by such factors as soil fertility, weather, and grazing management. The kind of herbaceous cover furnishing the competition, whether it be grass or forb, annual or perennial, influences the intensity of the relationship. The particular brush species may also aggravate or modulate the effect of competition. The competitive processes are the same with both sprouting and nonsprouting species. In sprouting brush, however, the control of seedlings is often not apparent because a new stand of brush will come from crown sprouts. These are little affected by grass competition.

In conclusion, the practice of reseeding following clearing of dense brush results in the application of a biological control measure on the subsequent brush population. The control mechanism, the grass cover, is, in addition, a good source of forage, a soil stabilizer, and an excellent fuel for fire in case additional clearing is desirable.

Summary

All the principles and processes involved in the grass density-brush seedling relationship can be considered collectively in Figure 18.

In this figure, the time scale radiates from left to right (mid-October to mid-August), each successive month covering more space to indicate the increasingly greater importance of the physiological processes operative on the plants throughout the season and their cumulative effects.

Grass density increases from 0 to maximum density clockwise along the arc and from left to right along the radii. In the first instance, density increases as the optimum rate of seeding is approached. In the second case, density increases as the plants tiller and grow larger in size. Grass seedling emergence, growth, phenology, and root development are represented to scale on the lower radius only.

Emergence of brush seedlings and their differential development and survival are represented to scale on both radii with implied intermediary conditions in the space of the angle between them.

Number of brush seedlings per unit—an area the width of a soil moisture column—indicates the number of seedlings per square foot anywhere along the time scale.

Each dot per square in a soil moisture column represents 0.1 per cent moisture above the estimated wilting point in a foot depth class.

Note that brush seedling roots in dense grass have not penetrated into zones of available late summer water; while those growing where there is no grass have reached depths beyond effective penetration of grass roots which might occur in subsequent years.

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STRATIFICATION IN WESTERN LAKE ERIE IN SUMMER OF 1953: EFFECTS ON THE HEXAGENIA (EPHEMEROPTERA) POPULATION

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Although the water temperature and chemical composition of western Lake Erie are usually uniform from top to bottom, occasionally there are short periods of temperature stratification during unusually calm warm weather. These have usually been of such short duration that no appreciable chemical or biological changes have been observed. Chandler (1940: 297; 1944: 204) reported such temporary thermal stratification in western Lake Erie in 1939 and 1940. Chandler and Weeks (1945: 437) found similar conditions in 1942. Wright and Tidd (1933: 273) reported temporary thermal stratification in the eastern part of the Island Section of Lake Erie. However, in this instance the temperature stratification was associated with a reduction of oxygen near the bottom where a low of 8.6 per cent saturation was reached.

Unusually low wind velocities prevailed in the Bass Islands region throughout the month of August and the first few days of September, 1953. The near calm conditions were especially pronounced during the period August 20 to Sept. 3, when the average velocity at Sandusky, Ohio, the nearest weather station, was below 4.3 miles per hour, with 13 miles per hour being the highest velocity observed during the period. Associated with this unusually calm weather were clear skies and high temperatures, in some cases exceeding the all-time records.

In this paper it will be shown that these conditions resulted in high water temperature and oxygen depletion near the bottom. This condition, in turn, resulted in changes in the bottom fauna.

Methods and Equipment

The temperature records were made with a bathythermograph that had been calibrated against an accurate stem thermometer. The water samples were collected in the Kemmerer water sampler. For samples near the bottom, the sampler was lowered until it touched the bottom, then it was raised a few centimeters and moved to one side before closing. In this position a vertical column of water about 42 cm. in length was collected a few centimeters above the bottom. The top of this vertical column may have been as much as 75 cm. above the bottom in some samples. Mortimer (1941-1942) showed that in some thermally stratified lakes oxygen depletion in the hypolimnion was greatest at the mud-water interface. Therefore, the quantity of oxygen at the true bottom, or mud-water interface, of Lake Erie was probably much lower than the results obtained in the samples. The Rideal-Stewart modification of the Winkler method was used for the oxygen determinations.

The 22.8 x 22.8 cm. Ekman dredge was used to obtain bottom samples. Four dredge hauls (⅕ sq. meter) were made at each station. Samples were taken only in mud bottom where this form of dredge performs most efficiently. The samples were washed in a screen of about twenty meshes per centimeter. The organisms removed were counted and preserved.

Physical and Chemical Conditions

Temperature recordings and oxygen determinations were made at stations A to H (Fig. 1). The temperature records and oxygen concentrations at the top and bottom are shown in Figure 2. These records indicate that temperature and oxygen stratification existed between September 1 and September 4. It is not known when these conditions began to appear, but it is probable that temperature stratification began during the last week of August, followed by a gradual depletion of oxygen near the bottom in the deeper water. Observed differences between the surface and bottom temperatures never exceeded 4° C.

In the several years that Chandler studied this part of the lake, he reported only one instance in which oxygen was below five parts per million. On September 7, 1938, he (Chandler 1940: 304) found that oxygen at the bottom was 4.94 p.p.m. Wright and Tidd (1933: 273) found low oxygen in only one instance in the two years of their study (1929 and 1930), but this occurred near the eastern boundary of the western end of Lake Erie. In contrast to this, all samples taken at the bottom in the deep water between September 1 and September 5, 1953, had less than 5 p.p.m. of oxygen. Stations G and H indicate that

[1] The writer wishes to thank Dr. David C. Chandler, Dr. Edward C. Kinney, Mr. James L. Verber, and Dr. Kenneth G. Wood for supplying valuable data included in this report.

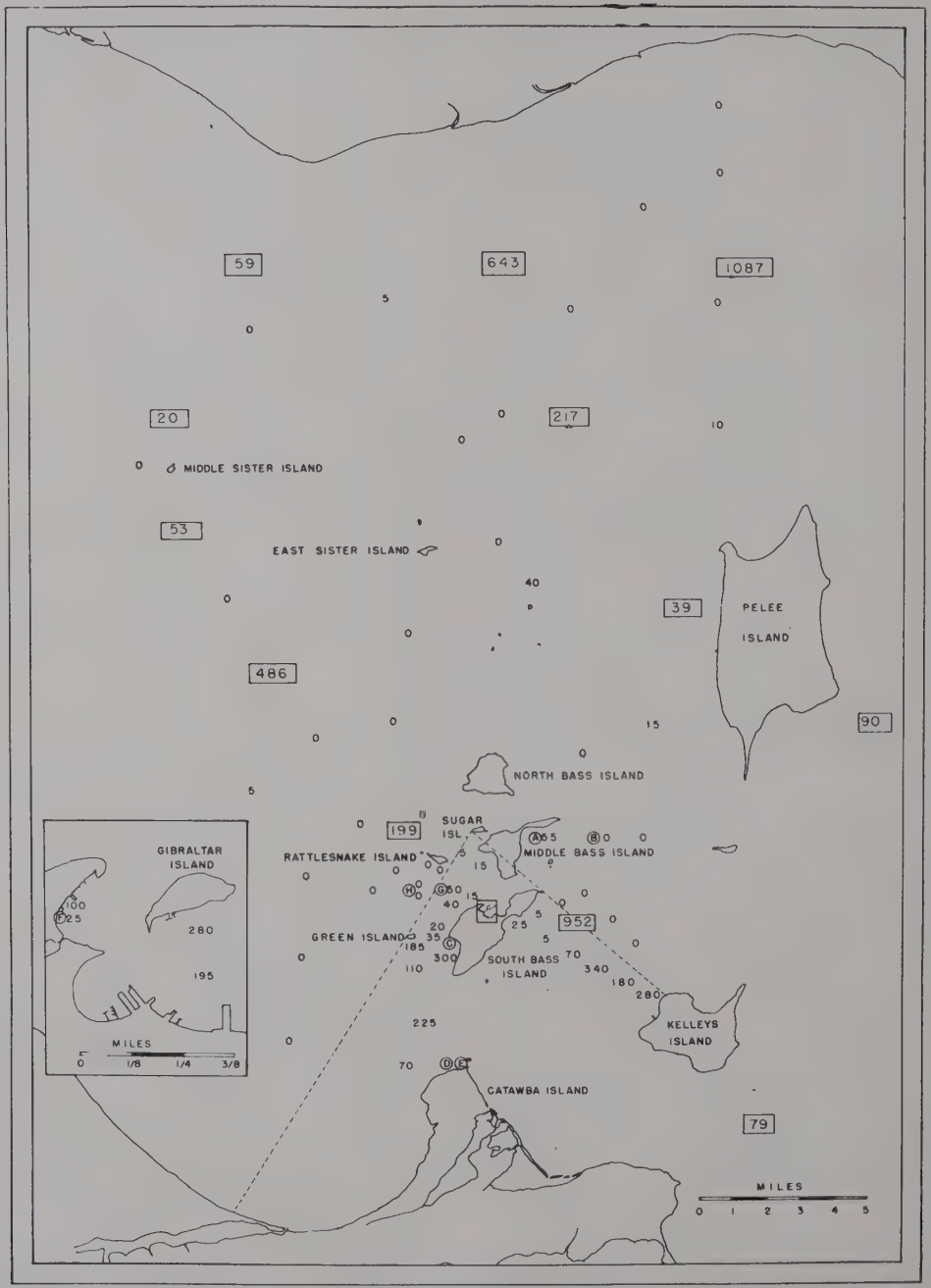

FIG. 1. Map of the Island Section of western Lake Erie. A to H, stations where temperature and oxygen were checked. Small numerals represent the number of living *Hexagenia* nymphs collected per square meter in this study. The larger numerals enclosed in rectangles represent the average number of living nymphs per square meter (from at least 10 samples in each area) collected by Wood in 1951-1952. Dashed lines enclose area where survival of nymphs was greatest.

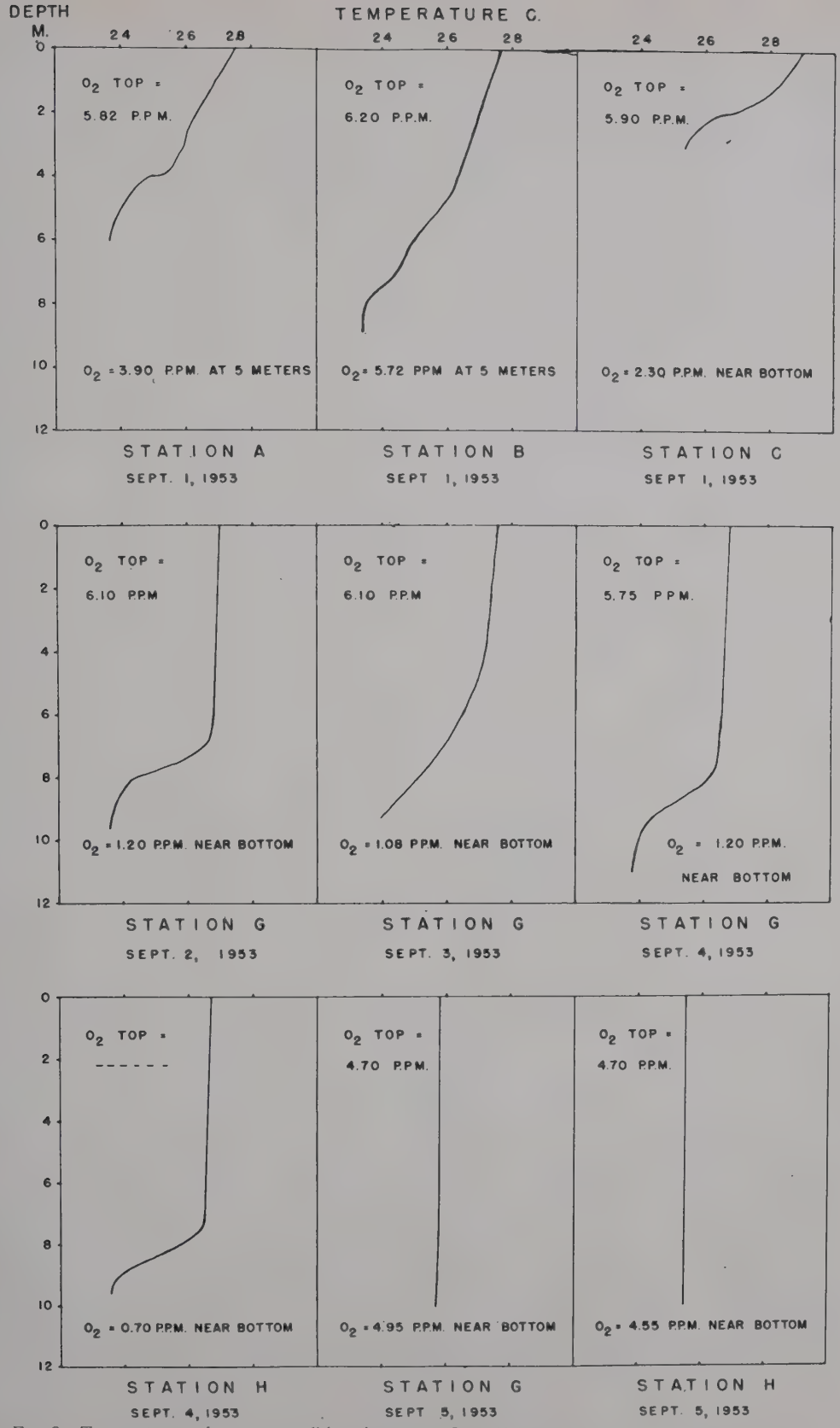

FIG. 2. Temperature and oxygen conditions in western Lake Erie on September 1-5, 1933.

oxygen depletion became gradually worse on succeeding days until circulation was restored on September 5.

The duration of the low oxygen conditions at the bottom is unknown. At station G the maximum value recorded for three days was 1.20 p.p.m. Station H had the lowest value, 0.70 p.p.m., but unfortunately, this station was sampled only once before the stratification was destroyed. It should be noted that even after circulation was again restored, the oxygen levels were low from top to bottom. This appears to be due to the dilution of the better aerated surface water by the low oxygen-content water from the bottom.

Effect on Hexagenia Population

Preliminary studies of the bottom fauna of the area showed that in some places the entire mayfly population, *Hexagenia rigida* McDunnough and *Hexagenia limbata occulta* (Walker), had been killed. Four dredge hauls (⅕ sq. meter) were taken at station H on September 5, at the time when the temperature and oxygen data were taken. The yield per square meter from this sample was 10 living Sphaeriidae, 5 living Hirudinea, 30 Tendipedidae (33% dead), and 465 *Hexagenia* nymphs (all dead). The dead *Hexagenia* nymphs were removed before the sample was processed in the screens. In the screening process, a high-pressure stream of water was used to break up the mud and force it through the screens. It is possible that this rough treatment may have been responsible for the dead Tendipedidae larvae. Some of the *Hexagenia* nymphs were bady decomposed, but were still intact. These nymphs decompose rapidly at high temperatures such as prevailed at that time; therefore, it was estimated that they had been dead only a few hours, or at most only a few days.

Since the population of *Hexagenia* nymphs had been completely destroyed at this particular station, it was desirable to determine the extent of destruction over a larger area. Obviously, the most satisfactory method of obtaining this information would have been to make extensive dredgings before the nymphs had decomposed. Dredging could not be resumed, however, until September 14. Thus at the prevailing temperature there was ample time for the decomposition of any nymphs that had been killed by the low oxygen conditions prior to September 5.

From September 14 to September 26 and on November 13, a total of 61 collections were made in the area between the Canadian Shore and Catawba Island on the south shore of western Lake Erie. Only the *Hexagenia* component of the samples has thus far been analyzed. The results are shown in Figure 1.

Out of a total of 61 collections, 32 (about 52%) contained no living *Hexagenia* nymphs. It should be noted that two subsequent collections from the area where the dead nymphs were found revealed no nymphs. The average number of living nymphs per square meter per collection for the 61 collections was only 44.3. If a line is extended from the west end of Sugar Island to the northwest end of Kelley's Island and another from Sugar Island along the west shore of Green Island to the south shore of the lake as in Figure 1, a total of 38 collections will be outside the acute angle and 23 inside it. The average number of living nymphs per square meter outside the angle was only 3.4 per collection. Inside the angle the average number per square meter was 112 per collection. These averages indicate that at that time a larger population per unit area was present in the relatively small area near the islands and the South Channel than was present in the larger more open areas of the lake. There are at least two possible explanations for this. Since the thermocline was usually below the 6-7 meter depth, the nymphs in the more shallow areas were not subjected to the extremely low oxygen conditions. The other explanation appears to be more complex. The studies on the currents of Lake Erie by Verber (1953) appear to show a movement of water from Sandusky Bay and vicinity into the island area. The survival of a larger population of nymphs in the channels may be due to these currents carrying water of higher oxygen concentration into these areas. Regardless of the cause of this survival, the area is rather small in comparison with the large open areas of western Lake Erie.

In order to show the extent of reduction in the mayfly population, it appears necessary to show that the area studied was previously inhabited by large populations of nymphs. Some data on this subject are found in previous studies made in this locality. Wright and Tidd (1933: 279) reported that in 1929 and 1930 the average number of *Hexagenia* nymphs in the Island Section of Lake Erie was 283 and 510 per square meter respectively. Wood (1953) made a survey of the bottom fauna of western Lake Erie. He used a front iron dredge similar to that described by Richardson (1922: 367-368). He made collections from May 9 to 31, 1951, and from September 24, 1951, to May 26, 1952. Using his conversion factor (0.09 sq. meter), the average volume of sediment per haul (16.3 liters), and the number of nymphs collected per haul, a rough estimate of

320 nymphs per square meter was obtained for the 150 collections made in the present study area. The averages for different parts of this area are shown on the map (Fig. 1). In one area 12 samples gave an average of over 1000 nymphs per square meter. In the present study no nymphs were found in this particular area. In the autumn of 1942 and 1943 Chandler (personal communication) made collections in the island area just south of Rattlesnake Island. The average number of *Hexagenia* nymphs per square meter from the three collections in 1942 was 493. The average for the three collections in 1943 was 351 per square meter.

The writer with the aid of his Limnology classes of 1952 and 1953 made collections in the same area. A total of 388 nymphs per square meter was collected on June 17, 1952. On June 23, 1953, a total of 300 nymphs per square meter was collected. Of the 300 nymphs, 284 were small first-year nymphs. Normally in Lake Erie these do not emerge until the following spring. Therefore, this population should have remained in the area until June or July of 1954. However, collections made on September 16, 1953, showed the nymphs to be absent from the area. Since this was near the area where the 465 dead nymphs were collected, it appears that these nymphs may have suffered a like fate.

Other evidences that the area sampled had recently been inhabited by the nymphs were the presence of deserted burrows in the mud dredged from most of the stations and the abundance of sclerotized parts of the nymphs.

A comparison of the average number of nymphs found in previous years with the numbers collected in this study shows population reductions ranging from a few per cent in limited areas to 100 per cent in much of the open lake.

The cause of the reduction is believed to have been the low oxygen concentration at the bottom, associated with relatively high temperature. Temperature at the bottom did not exceed 24° C. until September 5, when mixing brought the bottom temperature up to about 25.5° C. Even then, the bottom temperature in the deeper water was no higher than that near the shores where survival was greatest. *Hexagenia* nymphs have been kept alive for days in shallow pans of water in the laboratory where the air temperature was as high as 29° C. Therefore temperature alone does not appear to have been the cause of the destruction of the population.

Morgan and Wilder (1936: 168) studied oxygen consumption of the closely related mayfly, *Hexagenia recurvata* Morgan, in winter. They state that this species may survive when the oxygen concentration is as low as 0.50 cc. per liter of water. They showed the metabolic rate of this species to be low in winter and to vary with temperature. Since the highest average temperature used in their experiments was only 12.3° C., it is questionable whether or not their specimens could have survived the above oxygen concentration at temperatures of 24° to 25° C.

At station H on September 4, the oxygen concentration a few centimeters above the bottom was 0.70 p.p.m. or about 0.50 cc. per liter. The oxygen concentration in the mud and in the burrows is unknown, but it probably was much lower than that indicated by the water sample. Therefore, it appears likely that the low oxygen concentration at the bottom was the major cause of the reduction of the *Hexagenia* population in western Lake Erie.

The ultimate effects of the reduction of this population are unknown at the present time, but since these mayflies are known to form a large proportion of the food of several kinds of fishes in Lake Erie, this reduction could have a rather far-reaching effect on the fishes of the area.

Kinney (1950) studied the food of the trout perch, *Percopsis omiscomaycus* (Walbaum), which is an important forage fish in this area. He found that more than half of the adult stomachs from 22 collections contained only *Hexagenia* nymphs. In another case, *Hexagenia* nymphs constituted 96 per cent of the volume of the stomach contents of 162 specimens. Removal of *Hexagenia* from the food of this fish may result in a reduction in the population remaining in this area.

In a study now in progress, Kinney (personal communication) has compiled some comparative figures on the foods found in the stomachs of the silver chub, *Hybopsis storerianus* (Kirtland), another important forage fish in this area. The percentage of specimens containing any food was lower for the September and November collections in 1953 than for the comparable period of 1952. The percentage of specimens containing *Hexagenia* was much lower for 1953 than for the same period in 1952. The volume of *Hexagenia* as per cent of total stomach contents was 67.3 per cent in September 1952 as compared with 4.5 per cent in September 1953, a drop of almost 15-fold. For the month of November the drop was approximately 5-fold between the 1952 and the 1953 collections; however, the 1953 figures are based on a small number of large specimens which may not give a truly representative figure. As mentioned above, there was not only a drop in the *Hexagenia* component of the food of the silver chub, but also

a decrease in the percentage of fish that contained any food. This may indicate that the fish have not been able to find enough other food to replace the loss of *Hexagenia* in their diet. If this is true, then a reduced population of silver chub in this area may result.

At certain times, many of the commercial and sport species of fishes in Lake Erie eat large quantities of *Hexagenia* nymphs and adults. Although no specific data are available on this subject at this time, there is the possibility that such a reduction in the *Hexagenia* population may directly influence the feeding habits of these fishes. However, the indirect influence through the small forage fishes is probably more important.

It now appears that the whole economy of western Lake Erie may be affected to some extent by the short period of stratification. While some of the effects are known, the ultimate effects may be very complex, requiring a much longer period of study.

Summary

1. Unusual thermal stratification was observed in western Lake Erie during the period September 1-4, 1953.

2. Oxygen concentrations as low as 0.70 p.p.m. were found near the bottom.

3. Bottom samples collected on September 5, 1953, revealed a total of 465 *Hexagenia* nymphs (all dead) per square meter.

4. In 61 bottom collections made over a large area between the Canadian Shore and Catawba Island on September 14-26, and November 13, 1953, the average number of living nymphs per square meter was 44.3. This was much lower than averages found in other years.

5. The stomach contents of the silver chub, *Hybopsis storerianus* (Kirtland), showed a great reduction in the use of *Hexagenia* nymphs in September and November, 1953, as contrasted with the same period in 1952.

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DEVELOPMENT OF VEGETATION AFTER FIRE IN THE CHAMISE CHAPARRAL OF SOUTHERN CALIFORNIA

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Regrowth of the chaparral cover[2] in southern California after its removal by fire is a phenomenon of more than academic interest. Ecologists are interested because of the remarkable ability of the chaparral species to persist where fires are of common occurrence. Foresters and others who manage wild lands are interested because the return of vegetation on fire-denuded watersheds means reduction of the severe erosion hazard

[1] Maintained by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of California, Berkeley, California.

[2] "Cover" as used in this paper refers to all the vegetation growing on a given area, and does not refer to "density" or to "coverage" as generally used by ecologists.

which usually exists the first several years after a fire. In areas where grazing is practicable, stockmen are interested in the browse and forage value of the new growth, and in possible replacement of the burned brush with grass or other more palatable plants. In areas adapted to recreational use, many people are interested in establishing groves of trees, especially conifers, to enhance the recreational values. Finally, public officials and conservation agencies concerned with water yield and flood control in mountain watersheds are interested in improving the chaparral as watershed cover, whether by manipulation of the present cover or its ultimate replacement with vegetation that will be less inflammable, will consume less water, and yet will provide satisfactory control of erosion and floods. To all of these interests, some understanding of the behavior of the chaparral after fire is fundamental.

In 1927, the U. S. Forest Service started in southern California a study of the development of a chaparral cover after denudation by fire. This paper reports the results of that work, which continued to 1952. The study was concerned solely with chaparral types dominated by chamise (*Adenostoma fasciculatum*).[3] These types have been grouped under the general term "chamise chaparral," which can be defined as any shrub community containing chamise as an important dominant (more than 20 per cent of the cover density). This is one of the most abundant plant associations in the southern California mountains below 6,000 feet in elevation, occurring principally on the south-facing slopes, but occasionally on north-facing ones. The chamise chaparral varies from dense stands of chamise and ceanothus to open stands of chamise and black sage (*Salvia mellifera*). The commonest associated species are hoaryleaf ceanothus (*Ceanothus crassifolius*), several species of manzanita (*Arctostaphylos* spp.), and such small, shrubby species as the sages (*Salvia* spp.), and buckwheats (*Eriogonum* spp.).

In the southern California chaparral, fire usually consumes the crowns of vegetation as well as the litter on the ground. Many stems and branches an inch or more in diameter are left as snags. In places, the soil may be covered with ash, its depth depending upon the density of vegetation and the amount of litter. In chamise chaparral, the ash is sparse and usually confined to the bases of the shrubs.

The vegetation that follows fire in the chaparral is, broadly speaking, of two kinds—long-lived and short-lived (Fig. 1.) The long-lived species are referred to in this report as the "permanent" cover because they are the species which constitute the chaparral 10 years or more after a fire. They are mainly brush species, but intermingled with them are usually some subshrubs and, less commonly, vines. Many of these species sprout vigorously from buds in their root crowns after the tops are killed. Other species are killed outright by fire. With few exceptions seedlings of both kinds appear in the post-fire cover. Seed-

FIG. 1. Regrowth of vegetation after the Fern Canyon fire of November 1938: (top) Shortly after the fire had removed the original brush cover; (middle) the following spring showing an annual herb cover of *Phacelia brachyloba;* (bottom) four years later showing a dense cover of sprouting chamise, Eastwood manzanita (*Arctostaphylos glandulosa*), and chaparral whitethorn (*Ceanothus leucodermis*) stumps.

[3] Authors for scientific names of plants, if not given in the text, are shown in Tables IV, V, VI, and VII.

lings of species that fire-kill are usually much more abundant than those of the sprouting species.

The short-lived, or "temporary," cover is composed of annual herbs and herbaceous perennials, the latter consisting of perennial herbs and short-lived subshrubs. These plants develop from seeds germinated the first rainy season after the fire.

The Study

The chamise chaparral study presented in this paper was conducted on the south slopes of the San Bernardino and San Gabriel Mountains in western San Bernardino and eastern Los Angeles Counties, California (Fig. 2). The topography of both mountain ranges is rough, with precipitous canyons. The climate is Mediterranean in character, with hot, dry summers and cool, moist winters. In most years, no rain falls from May to October.

The mountains were formed by fault block uplifts. Much of the underlying rock is pre-Cretaceous metamorphic (Vaughn 1922) (Storey 1948), composed of gneisses and schists mixed with a large percentage of igneous dike rocks, mostly diorite, and, in the San Bernardino Mountains, slightly metamorphosed limestone. All the rocks are deeply fractured and weathered. The soils are shallow and are composed primarily of partially weathered rock particles. The erosion rate on the steep slopes is too high to allow the development of soil horizons. Thus, the soil character is determined largely by the composition of the underlying rock and by its susceptibility to weathering (Colman 1948).

Method of study

This paper is based upon data collected from permanent sample plots located on several areas burned by wild fires. No attempt was made on any of the burns to randomize the plot locations. Typical locations were chosen, but no plots were placed upon the steepest portions of the watersheds because of the difficulty of protecting the natural character of the vegetation from disturbance during periodic examinations.

Most of the plots were one milacre in size and were established either as single plots or as groups of adjoining plots. The earlier plots were square (6.6 feet on a side), but the later ones were rectangular (13.2 feet by 3.3 feet). Plot corners were marked by upright metal rods driven into the soil with 6 inches left exposed. The plots were usually established at the close of the first growing season after burning (about May) in order to make the observations before the annual herbs began to dry. The plots on the first burn studied, however, were not established until August of the second season.

In the first several years after burning, the plots were observed every year in May or June. Later they were observed at intervals of 2 to 5 years. The location of the perennial vegetation was mapped, and height and spread were recorded. The number per milacre and the average height of the annual herbs were also recorded.

In the early years of the study, only the total crown density[4] was estimated, but in the later years the density of the component species was also recorded. Densities in this shrub cover were hard to determine accurately, and estimates varied somewhat between observers. Therefore, during analysis of data, the proportion of vegetation cover to bare areas on the plots was checked against the spread of the plants as recorded or drawn on the field sheets, and against repeat photographs where these were available.

The study areas

The sample plots were established on seven different burns which occurred over a period of 17 years, in Waterman and Barranca Canyons north of the city of San Bernardino, and in Fern and San Antonio Canyons north of Claremont.

Location and fire history.—The 42-acre Barranca watershed is the site of the largest number of sample plots. This drainage is just east of Devil Canyon and about 7 miles north of the city of San Bernardino.

Before 1925, the Barranca area had undoubtedly been burned within a comparatively few years, but the fire records are incomplete. The southeast ridge of the watershed was partially burned on January 23, 1918. How far this fire burned into the study area is unknown. Small fires of about 20 acres in size occurred north and west of the watershed in 1911, 1912, and 1916. A 200-acre fire occurred south and east of the watershed in 1917. Any of the fires before 1918 might have burned portions of the study area but no conclusive evidence of such events was found on the ground.

The Barranca watershed was almost completely burned August 31, 1925. Twenty-seven sample plots of one milacre each were established in the burned area during August, 1927. Four plots were established in nearby brush that had not burned in 1925. On November 24, 1938 a fire approached the Barranca watershed from the east,

[4] "Density" as used in this paper refers to the per cent of the soil surface which would be shaded by specified plants in a plot or area if the sun were directly overhead. This corresponds to the ecological concept of "coverage" or "cover."

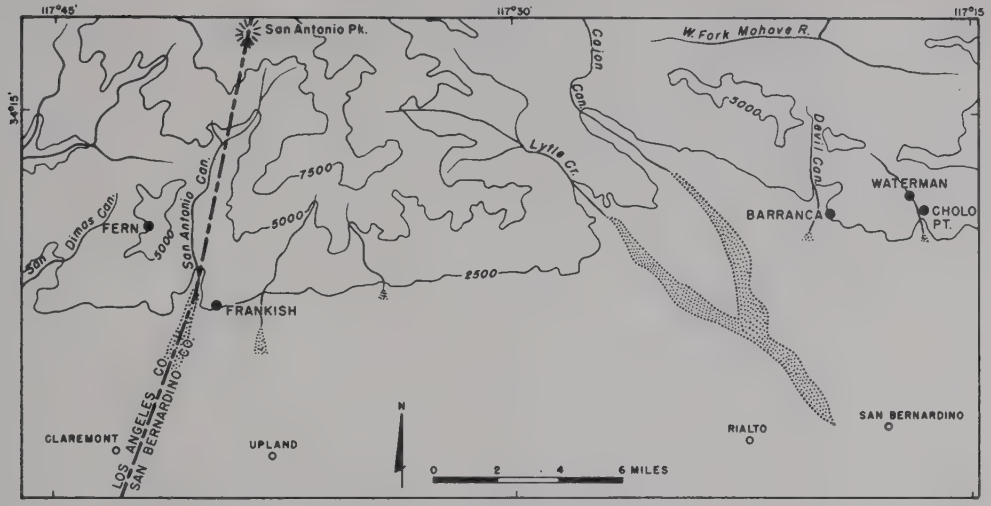

FIG. 2. Sketch map showing location of the study areas in San Bernardino and Los Angeles Counties, California.

burning a small portion of the watershed and two of the 1927 sample plots in unburned cover. Another fire on March 20, 1942, approached from the north and reburned two of the plots (burned previously in 1925) in the upper end of the watershed.

In Waterman Canyon, 6 miles north of San Bernardino, are two study burns. The first fire occurred on November 27, 1930. A rectangular plot, 2 milacres in size (3.3 by 26.4 feet), was established in the burned area the next spring. The second fire occurred at Cholo Point July 24, 1931. Two plots of the same size and dimensions were established there in the summer of 1931 before any rain fell on the burn.

The watershed of Frankish Canyon contains one study burn. This watershed is just east of San Antonio Canyon at the western edge of San Bernardino County, and about 5 miles north of Upland. The canyon burned September 16, 1935, and 4 rectangular 1-milacre (3.3 by 13.2 feet) sample plots were established there in May 1936. Fern Canyon (a tributary of San Dimas Canyon) 8 miles north of Claremont also has one study burn. On November 18, 1938 a large fire burned into the canyon from the east. Three rectangular 1-milacre plots were established in this burn at an altitude of about 5,000 feet in May 1939. This area had not been burned since about 1890.

Site characteristics.—The plot groups differ somewhat as to site characteristics (Table I). These differences would be expected to have some effect upon the vegetation and its regrowth after burning.

All except the Fern Canyon plots are located between 2,100 and 3,100 feet altitude. This 1,000-foot altitudinal range has no significant effect on composition of the cover, but the Fern Canyon plots, at 5,000 feet altitude, have quite different vegetation from those at lower altitudes.

The plot groups vary in exposure from south to northwest. The northwest-facing plots are all located on relatively flat ridge tops and therefore are not shaded as much as most steep north exposures. The slope gradients vary from 10 to 65 per cent, most of the plots being on the gentler slopes.

The soils occurring on the plots were derived from either igneous or metamorphic rocks and are typical of the southern California mountains. The soils vary in depth from 1 to 5 feet. This range of depths is usual for the chamise-chaparral association. In several cases, weathering has progressed slowly, and rock fragments several inches or more in size make up a large portion of the soil mass. The Barranca plots situated in chamise-manzanita and chamise-black sage are particularly rocky and have less soil material per foot of depth than the other plots.

Soil losses by erosion during the first few years after the removal of the brush cover by fire were measured in most plots as less than an inch in depth. On the steeper portions of the chamise-ceanothus-black sage type at Barranca, soil losses up to 2 inches were measured after the 1925 fire. The Cholo Point burn of 1931 was subjected to high-intensity rain soon after the fire. Soil losses here were 2 to 3 inches measured at the metal stakes, and gullies 5 to 6 inches deep were observed across the center of the plots.

TABLE I. *Physical characteristics of the sample plot groups*

Locality	Year of fire	Vegetation type*	Area of plot group (milacres)	Altitude (feet)	Exposure	Gradient (per cent)	Rock	Soil depth (feet)	Erosion† (inches)
Barranca	1925	Af-Cer	12	2400	NW	10-20	Diorite	2-4	0-1
Barranca	1925	Af-Cer-Sm	12	2100-2700	SW	35-65	Diorite	1-2	1-2
Barranca	1925	Af-Ag	1	3000	NW	25	Limestone	1.5	0-1
Barranca	1925 and 1942	Af-Cer	1	2700	S	45	Diorite	3.0	0-1
Barranca	1925 and 1942	Af-Sm	1	3100	W	25	Diorite	1.5	0-1
Barranca	1938	Af-Cer-Sm	2	2700	S	40	Diorite	2.0	0-1
Barranca	(No record)	Af-Cer-Sm	2	2300	SW	50	Diorite	2.0	..
Waterman	1930	Af-Cl	2	2700	NW	10	Diorite	3-5	0-1
Cholo Point	1931	Af-Cer-Cl	4	2500	S	40	Diorite	1-3	2-3
Frankish	1935	Af-Cer-Ac	4	2600	S	30	Gneiss	2-4	0-1
Fern	1938	Af-Cl-Agl	3	5000	SW	30	Gneiss	2-3	0-1

*Af - *Adenostoma fasciculatum*, Ag - *Arctostaphylos glauca*, Cer - *Ceanothus crassifolius*, Sm - *Salvia mellifera*, Agl - *Arctostaphylos glandulosa*, Ac - *Artemisia californica*, Cl - *Ceanothus leucodermis*.
†Total depth of soil loss for the first five years after burning.

Precipitation.—Regrowth of vegetation is affected also by moisture conditions during the first several years after the fire. Average annual rainfall for the period of plot observations varied from 24.2 inches at the lower elevation at Barranca to 33.3 inches at Fern Canyon. The Waterman area received 30.3 inches; Frankish Canyon, 26.6 inches. Inasmuch as the plot groups were established on burns which occurred in different years, the amount of rain received by the different plot groups during the first few years after the fires varied greatly. The first years after the 1925 Barranca fire were generally dry, with six years out of the first nine below the 24-year average. The Waterman and Cholo Point burns received somewhat more rain in the first seasons than Barranca. The Frankish Canyon plots received far above average precipitation in the second and third seasons after the fire, and somewhat below average in the first and fourth. Fern Canyon received large amounts of rain in the third and fifth years after the fire and below normal in the first and fourth. Since the winter of 1946-47, all areas have received slightly less than 60 per cent of average annual rainfall. In contrast, the winter of 1951-52 was much above average.

GROWTH OF VEGETATION ON THE STUDY PLOTS

At Barranca, the permanent cover that developed after burning ranged from dense chamise-ceanothus[5] stands to open stands of chamise-black sage, frequently with scattered ceanothus shrubs. The chamise-ceanothus type developed on sites with soils 2 feet or more in depth and on gentle slopes (Fig. 3). The chamise-black sage type developed on the drier sites with shallower soils and usually steeper slopes (Fig. 4). A third type, with chamise and bigberry manzanita (*Arctostaphylos glauca*) occurred in one small area with limestone rock.

Chamise individuals reached their greatest average 10-year height growth (38.2 inches) in

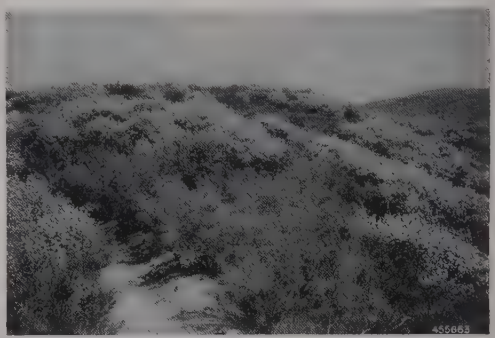

FIG. 3. Typical chamise-ceanothus type at Barranca watershed 21 years after burning. The shrubs in bloom are hoaryleaf ceanothus; those not in bloom are chamise.

FIG. 4. Typical chamise-ceanothus-black sage type at Barranca watershed four years after burning. The temporary vegetation has almost completely disappeared.

[5] When "ceanothus" is used in combination with chamise to designate a plant type in this paper, it always refers to the hoaryleaf ceanothus and not to chaparral whitethorn.

TABLE II. *Differences in cover developed upon the various plot groups*

Species or plant group	Barranca					Waterman	Cholo Point	Frankish	Fern
	1925 fire				1938 fire	1930 fire	1931 fire	1935 fire	1938 fire
	Af-Cer-type*	Af-Cer-Sm type	Af-Sm type	Af-Ag type	Af-Cer-Sm type	Af-Cl type	Af-Cer type	Af-Cer Ac type	Af-Cl-Agl type
	Average height growth, in inches, of dominant shrub 10 years after burning								
Adenostoma fasciculatum	38.2	33.9	14.7	12.5	25.7	49.0	44.2	51.3	45.0
Arctostaphylos glandulosa	....	....	....	....	....	....	47.0	....	35.0
Artemisia californica	....	....	....	....	....	....	....	29.9	....
Ceanothus crassifolius	43.3	38.4	....	....	38.8	....	53.2	42.7	10.7
Ceanothus leucodermis	....	....	....	....	....	25.9	28.4	....	28.5
Salvia mellifera	....	24.8	24.0	....	24.0	....	....	34.2	....
	Temporary cover - total number of individuals observed per milacre during entire period of study								
Herbaceous perennials	14.8	43.2	94.0	137.0	†	136.0	18.3	143.5	139.0
Annual herbs	286.3	216.9	353.0	27.0	†	54.0	1464.6	2533.9	538.2

*Af - *Adenostoma fasciculatum*, Ag - *Arctostaphylos glauca*, Cer - *Ceanothus crassifolius*, Sm - *Salvia mellifera*, Agl - *Arctostaphylos glandulosa*, Ac - *Artemisia californica*, Cl - *Ceanothus leucodermis*.

†The Barranca plots burned in 1938 were not visited yearly, and therefore the numbers of individuals would not be comparable with those of the yearly visited plots

the dense chamise-ceanothus (Table II). In the chamise-manzanita on soil derived from limestone, the plants were dwarfed. They grew only 12.5 inches high in 10 years. Wherever occurring at Barranca, the hoaryleaf ceanothus shrubs were somewhat taller than the chamise after 10 years.

In general, the temporary cover on the Barranca plots was not so dense as in the other study areas; perhaps this openness was due to the low rainfall occurring at this area during the first several years after the burn. The heaviest cover, in point of density and height growth, developed in the chamise-ceanothus type, with the chamise-ceanothus-black sage a close second. These temporary covers were predominantly annual herbs. The dwarf chamise-black sage type produced a more vigorous herbaceous perennial cover and many annual herbs. The latter, however, were small in stature (usually not over two inches in height). The temporary cover in the chamise-manzanita was composed primarily of herbaceous perennials.

The Waterman plots were located on a bench having deep soil. The permanent cover was composed entirely of chamise and chaparral whitethorn. The chamise had reached an average height of 49.0 inches in 10 years, more than 10 inches taller than the height reached in any Barranca group, and the chaparral whitethorn reached 25.9 inches. The temporary cover was composed mostly of herbaceous perennials of which *Penstemon spectabilis* was the dominant plant.

On the severely eroded Cholo Point plots, a dense stand of chamise (from sprouts) and hoaryleaf ceanothus (from seedlings) developed. The shrubs were vigorous, especially the hoaryleaf ceanothus which reached an average height of 53.2 inches in the first 10 years. This burn had many annual herbs, especially bromegrasses—a total of 1,464.6 per milacre for the period—but few herbaceous perennials, only 18.3 per milacre.

The climatic conditions at Frankish Canyon were ideal for the development of postburn vegetation, with above average rainfall in the second and third seasons after the burn and abundant spring rains in the first year. In addition to the vigorous chamise and hoaryleaf ceanothus, there were occasional large scrub oaks and such subshrubs as California sagebrush (*Artemisia californica*) and black sage. The burn had the most vigorous temporary cover of any studied, as indicated by an average of 143.5 herbaceous perennials and 2,533.9 annual herbs per mileacre. As at Cholo Point, the annual bromegrasses were the most numerous of the annual herbs.

The growth of shrubs on the 5,000-feet high Fern Canyon plots was quite similar to that of shrubs at lower altitudes, except that hoaryleaf ceanothus reached an average height of only 10.7 inches in 10 years. A vigorous temporary cover developed, averaging 677.2 individuals per milacre (Fig. 5). A large proportion of these individuals were coarse perennial herbs, *Nama parryi* and *Lupinus longifolius*.

Effect of fires upon the composition of the brush cover

From observations of the burned stumps taken during the first postfire year, it is possible to determine fairly accurately the number of individuals of the dominant species in the original cover. Only at Barranca, where recent fires burned plots established earlier, were records complete for the vegetation before the later fires.

FIG. 5. Temporary cover at Fern Canyon two years after the fire. *Nama parryi* (tall spikes in center) and *Lupinus longifolius* (left background) are the principal temporary species. Small seedlings of chaparral whitethorn and Eastwood manzanita are shown at center.

Before the burns, and considering all the plots, the average milacre had 4.4 individuals of chamise (Table III). On the average, two of these preburn individuals per milacre were killed by fire. Ten years after the fires an average of 2.4 individuals which had sprouted from the stump and one new seedling were alive. Thus, the fires reduced the average number of chamise shrubs per milacre from 4.4 to 3.4. It does not necessarily follow, however, that fire would eventually destroy this species, because in all plots where fewer than three shrubs grew per milacre before the fire, the number of individuals increased after the fire.

All individuals of hoaryleaf ceanothus were killed by the fires, but on every study burn except the 1942 reburn at Barranca, the number of surviving seedlings 10 years after the burn was greater than the number existing before (Table III). The average increase for all burns was from 0.9 shrub per milacre before to 2.4 shrubs after

TABLE III. *Average numbers of shrubs per milacre of two principal species before fire and 10 years after fire*

Locality and years of burns		*Adenostoma fasciculatum*				*Ceanothus crassifolius*	
		Before fire	10 years after fire			Before fire	10 years after fire
			By sprouts	Seedlings	Total		Seedlings
Barranca	1925....	4.5	2.0	1.3	3.3	1.3	2.1
Barranca	1925....	11.0	7.5	2.5	10.0	1.0	2.5
	1942....	10.0	8.0	0.5	8.5	2.5	0.0
Waterman	1930....	6.5	6.5	0.5	7.0	0.0	0.0
Cholo Point	1931....	5.5	2.5	0.0	2.5	0.3	2.7
Frankish	1935....	2.7	2.7	0.3	3.0	0.0	1.0
Fern	1938....	0.3	0.3	1.3	1.6	0.0	7.0
Barranca	1938....	1.0	1.0	0.5	1.5	0.5	3.5
Weighted average, all burns.....		4.4	2.4	1.0	3.4	0.9	2.4

the fire. The 1942 reburn occurred in March, and no seedlings developed in the short growing period between the fire and the dry summer, or thereafter.

It is probable that the temporary covers developed after repeated fires would vary owing to different conditions after the several fires. The two Barranca plots burned in August 1925 and again in March 1942 were the only plots where definite information was obtained. In the temporary covers on these plots, *Eriophyllum confertiflorum* was the most important dominant among the perennials after the 1925 fire, but *Convolvulus occidentalis* dominated after the 1942 fire (Table IV). *Stephanomeria virgata, Lotus strigosus,* and *Filago californica* were abundant annual herbs during the first several years after 1925. After that, *Bro-*

TABLE IV. *Maximum number of temporary-cover plants per milacre in any one year on two Barranca plots, burned in 1925 and 1942*

Species	After 1925 fire	After 1942 fire
Herbaceous perennial herbs		
Brassica incana (L.) F. W. Schultz	0.0	75.0
Convolvulus occidentalis Gray	26.0	51.0
Eriophyllum confertiflorum (D. C.) Gray	67.0	42.5
Helianthemum scoparium var. *vulgare* Jepson	7.5	0.0
Helianthus gracilentus Gray	4.0	10.5
Lotus scoparius (Nutt.) Ottley	24.0	38.5
Penstemon spectabilis Thurber	0.5	2.5
Annual herbs (Important species only)		
Bromus rubens L.	81.0	0.5
Bromus tectorum L.	0.0	10.5
Cordylanthus rigidus (Benth.) Jepson	0.0	10.5
Cryptantha intermedia (Gray) Greene	11.0	24.5
Filago californica Nutt.	24.0	2.5
Hugelia virgata var. *sapphirina* Jepson	12.0	6.0
Lotus strigosus (Nutt.) Greene	25.0	2.0
Oenothera micrantha Hornem.	5.5	17.5
Stephanomeria virgata Benth.	30.0	1.0

TABLE V. *Survival of shrubs and subshrubs after the fires*

Species	Type	Location	Years after burning									
			1	2	3	4	5	7	10	15	20	25
			Average number of plants per milacre									
Adenostoma fasciculatum H. and A.	Sprouts	Barranca	...	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.9
		Others	2.7	2.7	2.7	2.7	2.7	2.7	2.7	2.7	...	...
	Seedlings	Barranca	...	2.1	1.9	1.6	1.6	1.4	1.3	1.2	1.0	0.7
		Others	3.3	1.8	0.7	0.5	0.5	0.5	0.5	...	...	...
Arctostaphylos glandulosa Eastw.	Sprouts	Fern	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	...	...
	Seedlings	Fern	2.0	0.0	...	...	...	...	...	...	...	...
Arctostaphylos glauca Lindl.	Seedlings	Fern	2.7	2.3	...	0.7	0.7	0.7	0.7	0.0	...	...
Artemisia californica Less.	Seedlings	Frankish	3.2	2.2	2.0	2.2	2.0	4.9	4.1	14.8*	...	...
Ceanothus crassifolius Torr.	Seedlings	Barranca	...	3.3	3.0	2.9	2.8	2.5	2.0	1.6	1.3	0.7
		Cholo	8.0	7.2	6.5	6.0	5.8	4.5	3.6	...	...	...
		Frankish	1.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	...	...
		Fern	37.0	26.3	...	13.0	11.7	9.7	7.0	2.0	...	...
Ceanothus leucodermis Greene	Sprouts	Fern	0.3	0.3	...	0.3	0.3	0.3	0.3	0.3	...	...
	Seedlings	Waterman	38.0	32.3	12.3	8.0	8.0	7.0	3.7	...	...	...
		Cholo	6.5	6.2	4.5	4.5	3.0	1.8	0.6	0.0	...	...
		Fern	59.3	16.7	...	11.0	9.7	9.0	8.7	3.0	...	...
Eriogonum fasciculatum var. *foliolosum* Stokes	Seedlings	Barranca	...	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.08	0.08†
		Others	0.9	0.9	0.9	0.9	0.9	0.8	0.6	0.5	...	...
Salvia mellifera Greene	Seedlings	Barranca	...	2.5	2.5	2.4	2.4	2.3	2.2	2.2	2.1	1.6

*This figure is based on the 1952 observation or 17 years after burning. It includes the many seedlings developed during the wet season of 1951-52.
†These are new seedlings; the plants recorded in the previous column were dead.

mus rubens became very prominent. None of these annual herbs was important after the second burn, when *Cryptantha intermedia* and *Oenothera micrantha* were the early dominants and the perennial *Brassica incana* the later.

Survival and growth of permanent species

Chamise (*Adenostoma fasciculatum*) was common in all plot groups. Both the sprouts from the root crowns and seedlings became important parts of the permanent cover. Only one sprouting root crown per 10 milacres died in 25 years at Barranca (Table V).

The shoots from the surviving root crowns grew rapidly during the first five years; after that, growth slowed down until it almost ceased at 20 years (Table VI). That mature chamise plants grow slowly was also shown by measurements on

TABLE VI. *Height growth of shrubs and subshrubs after the fires*

Species	Type	Years after burning									
		1	2	3	4	5	7	10	15	20	25
		Average height in inches									
Adenostoma fasciculatum H. and A.	Sprouts	19.1	26.1	28.4	32.6	33.6	34.8	37.8	38.6	40.4	40.5
	Seedlings	2.4	4.6	5.1	6.7	7.8	9.7	11.9	17.0	23.5	31.9
Arctostaphylos glandulosa Eastw.	Sprouts	9.0	17.5	25.0	27.5	30.7	36.8	38.0	40.0	....	....
Arctostaphylos glauca Lindl.	Seedlings	1.0	5.5	....	6.5	6.0	9.4	15.5	....	....	....
Artemisia californica Less.	Seedlings	2.7	9.1	16.3	19.3	21.1	24.1	29.9	6.4	....	....
Ceanothus crassifolius Torr.	Seedlings	4.1	7.5	12.9	18.4	25.1	35.0	42.4	57.2	82.7	87.3
Ceanothus leucodermis Greene	Sprouts	6.0	21.0	....	30.0	30.0	50.0	84.0	70.0	....	....
	Seedlings	2.5	8.3	11.6	14.6	15.6	18.0	24.7	30.7	....	....
Eriogonum fasciculatum var. *foliolosum* Stokes	Seedlings	....	3.0	10.1	16.9	15.9	16.5	16.6	20.7	20.0	....
Quercus dumosa Nutt.*	Sprouts	....	....	42.0	42.0	47.0	55.0	58.7	80.0	132.0	150.0
Rhus ovata Wats.*	Sprouts	....	30.0	30.0	32.0	30.5	32.7	33.5	36.2	35.0	39.5
Salvia mellifera Greene	Seedlings	....	10.3	13.6	18.5	22.4	23.9	23.9	27.9	29.8	31.6
Styrax officinalis L. var. *fulvescens* (Eastw.) M. and J.*	Sprouts	....	42.0	42.0	45.0	31.0	38.7	37.5	30.7	33.0	26.0

*Based on one or two individuals which lived throughout the study period.

the pair of plots established in 1927 in old cover: average height of the chamise shrubs in 1927 was 49.0 inches; in 1938 it was 53.0; and in 1949, 53.8.

Chamise seedlings developed only during the first rainy season after the fire, and no new seedlings were recorded in later years. Many of these seedlings died in subsequent years; but the survivors had reached an average height of 31.9 inches and were still growing 25 years after the fire.

Hoaryleaf ceanothus (*Ceanothus crassifolius*) was likewise common. All preburn individuals were killed by the fires, but usually many seedlings developed in the first post-fire year (Fig. 6). Many of the seedlings died in the first several years. At Fern, the decrease was from 37.0 seedlings per milacre the first year to 11.7 seedlings the fifth year. After the fifth year, there was a slow, gradual decrease in numbers. At Barranca during the recent years of low rainfall (1946-51), deaths increased until nearly half of the shrubs had died between the 20th and 25th years. Sometimes these deaths opened up the formerly dense stand, leaving openings 5 to 8 feet across (Fig. 7). Only three seedlings of hoaryleaf ceanothus appeared after the first year; all three were at Barranca. One of the three developed 10 years after the fire, and two 24 years after the fire. These seedlings all died in their first summer. Growth rate of this species was uniform while plants were young. Height growth amounted to about 5 inches a year, with some fluctuation due to site and climatic conditions. After 20 years there was a decrease in the growth rate.

Eastwood manzanita (*Arctostaphylos glandulosa*) sprouted vigorously from the root crown and grew rapidly for the first 3 years, but this growth rate was not maintained thereafter. Seeds germinated after the fire, but no seedlings on the sample plots survived the second year.

Bigberry manzanita (*Arctostaphylos glauca*) was killed by fire, and no sprouting occurred. Seedlings, however, were abundant after the fires

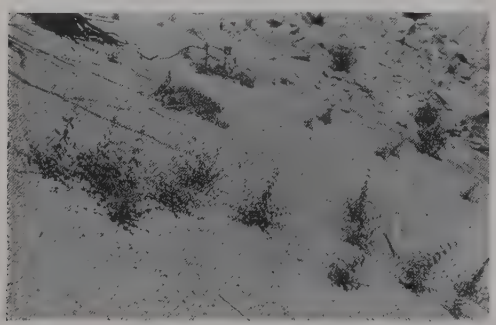

FIG. 6. Two-year-old hoaryleaf ceanothus seedlings.

FIG. 7. Death of hoaryleaf ceanothus at Barranca watershed has opened up the formerly dense cover and encouraged development of annual herbs. Photograph taken 24 years after burning.

No seedlings occurred on the sample plots at Barranca, but seedlings nearby made an average growth of three feet in 25 years. Growth at Fern was somewhat better—16 inches in 10 years—but none of the seedlings on these plots survived the recent years of low rainfall.

California sagebrush (*Artemisia californica*) occurred only at Frankish Canyon where it forms a sizable portion of the mature cover. All of the individuals developed from seed; no sprouting stumps were observed. The seedlings bloomed in the third season, and new seedlings appeared in the fourth year and in favorable years thereafter. The largest number observed was in 1952 (17 years after the fire) after the 1951-52 winter of high rainfall.

Chaparral whitethorn (*Ceanothus leucodermis*) reached its best development in the higher altitudes. At Fern Canyon, the stump sprouts grew vigorously and reached a maximum height of 7 feet in 10 years. Seedlings were very numerous and formed a substantial part of the cover. However, the recent dry years caused the death of a large portion of these seedlings, leaving some sizable openings in the cover. At Waterman and Cholo Point chaparral whitethorn was abundant, but the growth rate was slower than at Fern Canyon.

California buckwheat (*Eriogonum fasciculatum* var. *foliolosum*) formed a minor part of the cover on all the study burns, though it was not recorded at either the Waterman or Fern plots. At Barranca, the original plants had died by the 25th year, but new seedlings were occasionally observed even 25 years after fire.

Two individuals of California scrub oak (*Quercus dumosa*) were included in the plots: one at Barranca and one at Frankish Canyon. (Table VI records the growth of the Barranca shrub only.) Growth of these stump sprouts was espe-

cially rapid during the first three years. No seedlings of this species were noted at any time.

Sugarbush (*Rhus ovata*) occurs as scattered individuals throughout the chamise chaparral below 4,000 feet. Several large individuals whose root crowns sprouted vigorously occurred on the Barranca plots. During dry years, the branches died back, but during moist years sprouts grew from the stems. Thus, after the second year, the shrubs increased but little in size. No seedlings were found.

Black sage (*Salvia mellifera*) was most important at Barranca. Many individuals of this species remain as suppressed understory shrubs; only a few were killed during the drought years between 20 and 25 years after burning. All of the individuals in the study areas developed from seedlings although elsewhere sprouts from the root crowns have been observed after light burns. Height growth was rapid, and blooming started at about the third year. After blooming, the flowering stems died and new ones formed from the woody stems, usually not over 12 inches from the ground. The height reached each year by these flowering shoots seemed to depend upon the amount of rainfall and of competition from the associated shrubs. As the competing woody shrubs grew in height, the black sage shoots tended to be longer, though more sparse. Much of the growth increase recorded in Table VI probably was due to this reaction to crowding.

One shrub of California styrax (*Styrax officinalis* var. *fulvescens*) occurred in the chamise-manzanita plot at Barranca. After the first rapid growth, dieback of this shrub was greater than growth; 25 years after burning, the height was less than at the second year.

Besides these more important species of the permanent cover, a few woody species occurred as scattered plants without appreciably increasing the density of the mature stand. Two of these minor species are chaparral shrubs which occurred only as seedlings arising from seeds germinating several years after the burn. Seedlings of *Rhamnus crocea* var. *ilicifolia* (Kell.) Greene and *Prunus ilicifolia* Walp. appeared at both Barranca and Frankish Canyon.

Galium nuttallii Gray, *Galium angustifolium* Nutt., and *Lonicera johnstonii* (Keck) McMinn are fairly common woody, vine-like shrubs at Frankish Canyon. All sprouted vigorously from the root crown and sent up long shoots which climbed into the crowns of the woody shrubs.

Salvia apiana Jepson, *Trichostema lanatum* Benth., and *Yucca whipplei* Torr.[6] occurred at Barranca on the soils formed from limestone rock. At Frankish Canyon, scattered *Salvia apiana* occurred in the portions of the chamise chaparral containing *Artemisia californica*.

Eriodictyon trichocalyx Heller occurred on the plots at Cholo Point as sprouts from underground rootstocks. No seedlings of this species were found on any of the plots.

Survival and growth of temporary species

Of the herbaceous perennials, *Lotus scoparius*, *Lupinus longifolius*, *Nama parryi*, and *Senecio douglasii* are large subshrubs with woody bases (Fig. 8). Most of these reached flowering size by the second summer, and seeds were spread abundantly. New seedlings of the *Lotus* and *Senecio* appeared in subsequent seasons (Table VII). No new seedlings were recorded from the abundantly produced seeds of *Lupinus longifolius* and *Nama parryi*. These latter two species were short-lived, and had completely disappeared from the natural cover 5 years after burning. The *Lotus* and *Senecio* were longer-lived, and were numerous up to 10 or 15 years after the burn. In addition, some of the seedlings of *Lotus* which germinated in large intershrub spaces 15 years after the fire grew into plants 20 inches high, and were producing abundant flowers 20 years after the fire.

Eriophyllum confertiflorum, *Hazardia squarrosa*, and *Helianthemum scoparium* var. *vulgare* are small subshrubs rarely measuring over two feet in height. Many seedlings of the first two species developed from seeds dropped from plants which developed the first season after the fire. Few seedlings of *Helianthemum* other than the original post-fire plants were observed on the plots.

Dicentra chrysantha and *Penstemon spectabilis* are coarse perennial herbs which die down nearly to the ground every summer after blooming. They

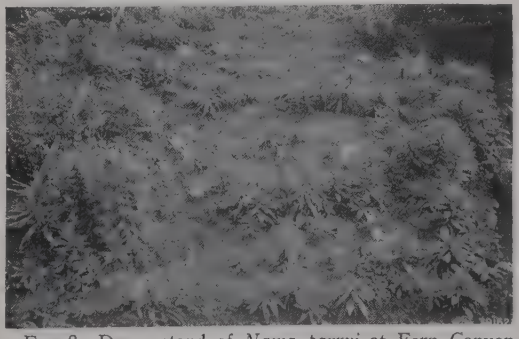

FIG. 8. Dense stand of *Nama parryi* at Fern Canyon one year after burning. *Lupinus longifolius* visible at the left.

[6] Neither of the two Yucca seedlings appearing in 1927 and 1932 had bloomed by 1949.

TABLE VII. *Occurrence of herbaceous perennials and annual herbs after the fires*

Species	Location	Years after burning									
		1	2	3	4	5	7	10	15	20	25
Herbaceous perennials		*Average number of seedlings per milacre*									
Convolvulus occidentalis Gray	Barranca	....	5.6	1.7	0.2	0.1	0	0	0	0	0
Dicentra chrysantha (H. and A.) Walp.	Barranca	....	0.6	0.6	0.2	0.1	0	0	0	0	0.2
Eriophyllum confertiflorum (D. C.) Gray	Frankish	2.5	2.0	21.8	68.5	26.2	4.5	4.4	1.0	...	...
Hazardia squarrosa Greene	Frankish	3.5	4.5	4.5	7.0	5.0	3.3	2.1	1.2	...	...
Helianthemum scoparium v. *vulgare* Jepson	Waterman	10.0	8.5	2.0	1.0	1.0	1.5	0	0	...	...
Helianthus gracilentus Gray	Barranca	....	0.5	0.5	0.8	0.9	0.8	0.1	0	0	0
Lotus scoparius (Nutt.) Ottley	Barranca	....	2.7	2.4	1.4	0.8	1.3	0.4	0.1	0.1	0
	Frankish	16.5	5.2	4.0	4.8	3.0	1.1	1.6	0	...	...
Lupinus longifolius (Wats.) Abrams	Fern	32.3	8.7	....	1.3	0	0	0	0	...	...
Nama parryi Gray	Fern	105.0	18.0	....	1.3	0	0	0	0	...	...
Penstemon spectabilis Thurber	Barranca	....	4.8	9.5	3.2	0.8	0.1	0	0	0	7.6
	Waterman	105.0	123.0	112.0	57.5	41.5	12.5	0	0	...	...
Senecio douglasii DC	Barranca	....	0.2	0.3	0.3	1.0	0.4	0.2	0.2	0	0.1
Annual herbs											
Brassica nigra (L.) Koch	Frankish	19.2	39.5	20.2	4.0	0	0	0	0	...	...
Bromus rubens L.	Barranca	....	0.2	9.0	16.8	40.3	1.8	0.4	0.1	0	0.2
	Frankish	0.2	8.0	151.5	423.5	106.0	30.5	10.8	24.6	...	...
	Cholo	0	2.0	293.8	232.0	99.2	93.8	0.2	...	...	...
Bromus tectorum L.	Frankish	0.2	0	8.2	34.0	101.0	63.0	11.2	5.0	...	...
	Fern	0	6.0	....	202.0	135.0	56.6	0.9	0	...	...
Chorizanthe staticoides Benth.	Frankish	0.5	3.8	5.0	26.0	24.2	17.9	30.9	4.7	...	...
Cryptantha intermedia (Gray) Greene	Barranca	....	2.5	11.1	3.7	20.7	0.7	0.6	0.1	0	0.6
Emmenanthe penduliflora Benth.	Barranca	....	0.8	0.2	0.4	0.1	0	0	0	0	0.5
	Frankish	23.8	2.2	0	0	0	0	0	0	...	...
Eriogonum gracile Benth.	Barranca	....	0.5	1.3	2.8	6.9	0.1	0	0	0	0
Eriogonum thurberi Torr.	Barranca	....	0	2.8	0.9	0.3	0	0	0	0	0
Festuca megalura Nutt.	Fern	0	0	....	13.7	18.0	7.8	0	0	...	...
Gilia gilioides (Benth.) Greene	Cholo	1.8	74.0	2.2	7.5	17.0	0	0	...	...	...
Hugelia virgata var. *sapphirina* Jepson	Frankish	0	5.2	33.0	13.0	18.2	9.3	4.5	1.3	...	...
Lessingia glandulifera Gray	Barranca	....	0.1	3.2	1.7	7.9	0	0	0	0	0
Lotus strigosus (Nutt.) Greene	Cholo	0.2	38.8	103.0	78.2	6.0	0	0	...	...	...
	Frankish	27.2	4.0	3.2	13.5	0.5	2.2	0	0	...	...
Oenothera micrantha Hornem.	Barranca	....	0	1.8	2.9	9.9	0.3	1.2	0.3	0	5.3
Phacelia brachyloba (Benth.) Gray	Waterman	29.0	3.0	0	0	0	0	0	...	...	...
	Cholo	0.5	81.2	0	0	0	0	0	...	...	...
	Fern	22.3	0	0	0	0	0	0	0	...	...
Phacelia minor (Harvey) McBr.	Barranca	....	10.8	0.7	0	0	0	0	0	0	0
	Frankish	5.0	32.0	2.2	0.2	0	0	0	0	...	...
Pterostegia drymarioides F. & M.	Frankish	2.2	1.2	2.8	12.2	1.0	6.1	16.7	1.7	...	...
Salvia columbariae Benth.	Barranca	....	0.1	1.0	1.2	6.1	3.0	0.3	0.1	0	0
Stephanomeria virgata Benth.	Barranca	....	18.7	19.7	4.6	4.9	0.1	0	0	0	0

rarely lived more than 5 years, but numerous new seedlings developed during the years before the permanent cover became dense. A striking reappearance of the *Penstemon* occurred at Barranca in the 25th year when an average of over 7 plants per milacre developed. None of these, however, lived to produce flowers.

Another perennial herb especially abundant at Barranca was the prostrate *Convolvulus occidentalis* which formed a large part of the ground cover in the second season. No new seedlings were recorded, and the species had disappeared by the seventh year.

Helianthus gracilentus, abundant in the drier plots at Barranca, persisted for about 10 years.

Certain other species of perennial herbs not included in Table VII were abundant in small areas. Liliaceous plants such as *Brodiaea capitata* Benth. and *Calochortus plummerae* Greene grew rapidly and some bloomed the first year, apparently from bulbs already present in the soil. Many new plants developed from seed, but as the cover matured the bulbs sent up a leaf only during moist seasons. It is probable that if the area were reburned, all the dormant bulbs would renew activity and many would bloom the first year.

At Frankish Canyon, two perennial bunchgrasses (*Melica imperfecta* Trin. and *Stipa lepida* Hitchcock) were common. The bunches were not killed by the fire, and removal of the chaparral cover was followed by rapid growth of the old clumps and the formation of new ones by seeding. As the chaparral cover matured, these grasses became suppressed and unimportant. At no time did they form a solid cover or become an important part of the vegetation on the burn as a whole.

Gnaphalium beneolens Davidson and *G. decurrens* var. *californica* Gray grew vigorously after the burn. Many new plants developed from seed in the third to fifth year, but even at Frankish Canyon where they were common, the species were of minor importance because of the small size of the individuals.

Brassica incana (L.) F. W. Schultz appeared at Barranca after the 1942 burn. This perennial or biennial exotic is now common throughout the area along trails, firebreaks, and other open areas in the chaparral.

Lomatium lucidum (Nutt.) Jepson, *Paeonia brownii* Dougl., *Scutellaria tuberosa* Benth., and *Solanum xantii* Gray occasionally occurred as scattered plants in mature chamise chaparral. They showed increased growth after burning but no new seedlings. The same was true of *Orobanche fasciculata* Nutt. and *O. tuberosa* (Gray) Heller which are parasites on chamise roots.

The following species occurred on the plots, usually as single individuals; they were not a sufficiently important part of the cover to discuss further:

Arabis holboellii var. *arcuata* Jepson
Chlorogalum pomeridianum Kunth.
Corethrogyne filaginifolia var. *rigida* Gray
Erigeron foliosus Nutt.
Malacothrix saxatilis var. *tenuifolia* (Nutt.) Gray
Selaginella bigelovii Underw.

Some of the annual herbs developed most abundantly in the first several years after the fire and then disappeared (Table VII). Other species were inconspicuous for the first years but reached their greatest abundance in 3 to 5 years after the burning. Some species, particularly those of the latter group, reappeared in later years when moisture conditions were favorable.

Phacelia brachyloba, Phacelia minor, Emmenanthe penduliflora, and *Stephanomeria virgata* were most abundant or vigorous during the first several years. *Phacelia brachyloba* is the most striking of these "fire-type" annuals. Between 1934 and the 1938 fire, the Fern Canyon area had been thoroughly botanized and only a few plants of this species were observed. These occurred in shaded sites along the intermittent stream channels. None was seen in the chaparral areas, even on firebreaks or along trails. After the fire this species was abundant everywhere. By the third year after burning, the species had reverted to its former rare status. The inference, of course, is that the seeds which germinated in the spring of 1939 had been formed after the last previous fire, probably more than 50 years ago. The other species listed, while more common in cleared areas and in the other plant associations, are similar "fire-type" species. *Stephanomeria virgata* was strikingly different from most of the annual herb species found on burns in that it grew principally in the summer. In fact, individuals frequently reached a height of six feet at maturity in October (Fig. 9).

The annual herbs which grow naturally on rock outcrops and in openings in unburned chaparral reached their maximum numbers more slowly on the study burns. *Oenothera micrantha* is an excellent example. It was three years before any plants of this species appeared on the Barranca plots. Their maximum abundance was reached in the fifth year, but 25 years after the fire the species was again numerous after having been almost completely absent for some time. Other species which behaved similarly are *Chorizanthe staticoides, Cryptantha intermedia, Hugelia virgata* var. *sapphirina,* and *Salvia columbariae.* These species, which apparently are not true "fire-type"

FIG. 9. Seedlings of the annual herb *Stephanomeria virgata* at Barranca the second season after burning. Seedlings of hoaryleaf ceanothus and *Phacelia brachyloba* in foreground.

plants, were observed to invade the study areas. They obviously were spreading from roads, trails, and openings in the chaparral. During the first season, they were to be found only near the spots where they were growing before the fire. By the third year they were well-distributed over the burn. It is probable that seeds of these species do not remain viable for long periods but depend upon a continued succession of plants for their production. At the latest inspection of the study areas, individuals of all these species were found in open areas in the chaparral.

The annual grasses, *Bromus rubens, Bromus tectorum,* and *Festuca megalura* were likewise slow in developing. These species are plants introduced from other parts of the world, and before the fires they were found only along trails, firebreaks, and openings. The greatest abundance of annual grasses was reached in the third to fifth year. They tapered off slowly as the brush cover matured.

Brassica nigra was sown for erosion control on the Frankish Canyon and Fern Canyon burns. Only at the former did this species appear on the plots. The maximum number of individuals appeared the second year; by the fifth year the species had completely disappeared.

Many other species of annual herbs appeared, especially at Frankish Canyon, but were too scattered to be given consideration in this paper beyond listing as follows:

Anagallis arvensis L.
Antirrhinum coulterianum Benth.
Apiastrum angustifolium Nutt.
Bromus rigidus Roth
Centaurea melitensis L.
Chaenactis artemisiaefolia Gray
C. glabriuscula DC
Chorizanthe parryi Wats.
Cryptantha micromeres (Gray) Greene
Ellisia chrysanthemifolia Benth.
Erigeron canadensis L.
Erodium cicutarium L'Her.
Eschscholtzia caespitosa var. *hypecoides* Gray
Eulobus californicus Nutt.
Festuca octoflora Walt.
Festuca reflexa Buckl.
Filago californica Nutt.
Gilia achilleaefolia Benth.
Gilia tenuiflora Benth.
Hemizonia wrightii Gray
Heterotheca grandiflora Nutt.
Lactuca scariola L.
Lupinus hirsutissimus Benth.
Malacothrix clevelandii Gray
Mentzelia micrantha T. and G.
Mimulus brevipes Benth.
Navarretia atractyloides (Benth.) H. and A.
Oxytheca trilobata Gray
Phacelia hispida Gray
Rafinesquia californica Nutt.
Scrophularia californica Cham.
Sonchus oleraceus L.

Changes in cover density

In general, the cover density on the study plots showed an early peak in 2 to 5 years after fire, then a temporary decline, a second and higher peak in 8 to 17 years, and thereafter a gradual decrease. The temporary vegetation developed rapidly in the early years, but usually died before being completely replaced by the permanent cover. This behavior of the herbaceous vegetation produced a temporary peak and decline in over-all cover density in all areas except Barranca (Fig. 10). The time of the first peak in each area depended upon the dominant species in the temporary cover. The annual herbs at Cholo Point, and the *Lupinus* and *Nama* at Fern Canyon reached their highest density in the second year, the *Penstemon* at Waterman in the third year, and the *Lotus* and *Hazardia* at Frankish Canyon in the fifth year.

At Barranca, the over-all cover density for all plot groups after the 1925 fire showed no marked early peak (Fig. 10). When cover densities are considered for the individual plot groups, however, slight early peaks are in evidence for all of them (Fig. 11). Because the peaks occurred in different years, the net result was to produce a period of several years with little change in over-all density.

The recent series of dry years (1946-51) was accompanied by decreased densities. This was especially noteworthy at Barranca where there was a marked decrease in recent years. Part of this was due to death of the hoaryleaf ceanothus shrubs and part to thinning of the crowns due to increased leaf fall and little or no new growth. A similar decrease was noted at Fern Canyon due to the death of chaparral whitethorn.

Discussion

Review of literature

The chaparral of California has long been recognized as a distinctive plant formation. Schimper (1903) and Warming (1909) described the chaparral as sclerophyllous woodland, and related the California formation to similar sclerophyllous types elsewhere in the world and to contiguous vegetation in California. Most of the early California writers were concerned with describing the mature brush stands and their relation to fire.

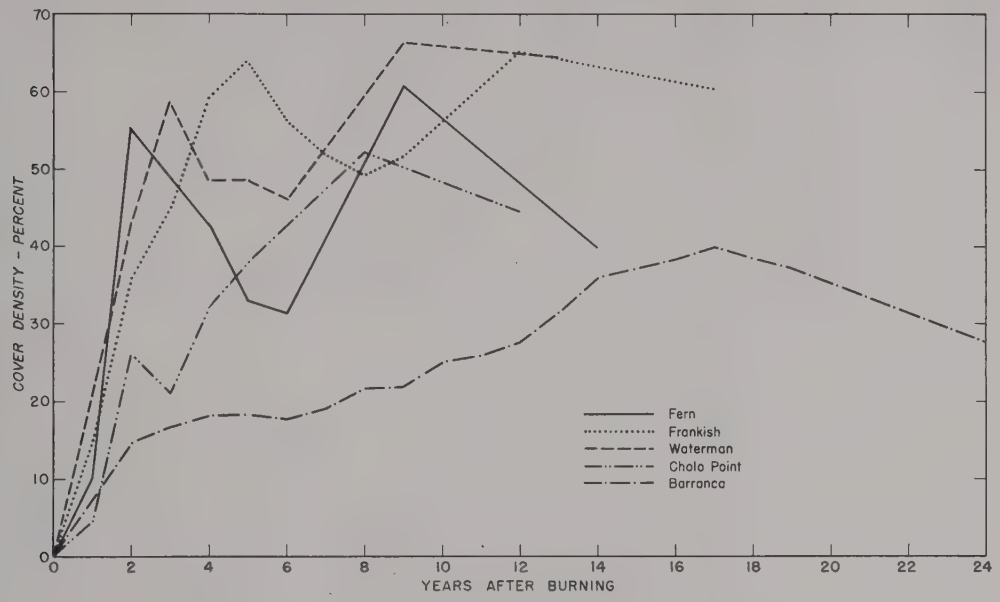

FIG. 10. Development of vegetative cover on the various burns.

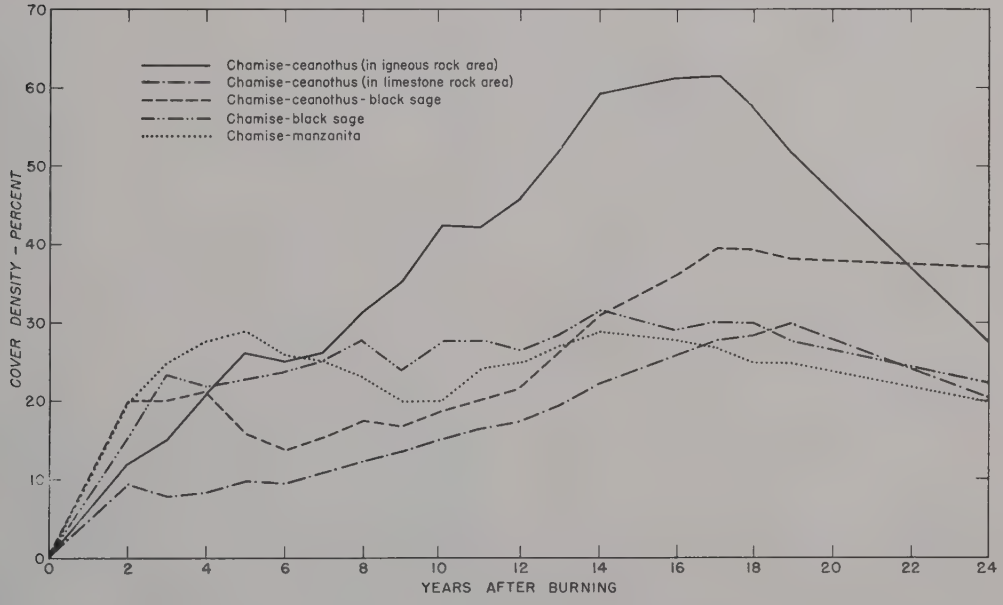

FIG. 11. Development of vegetative cover at Barranca.

Leiberg (1900) described in some detail the chaparral in the San Gabriel, San Bernardino, and San Jacinto Mountains, and concluded that its presence can be ascribed to a combination of severe climate and frequent fires. He also stated that the recovery of chaparral after burning is rapid.

Kinney (1900) discussed chaparral as a watershed cover, and stressed the great flood hazards occurring after the cover is removed by fire. Miller (1906) and Plummer (1911) gave similar descriptive material on the formation, and likewise stressed the great flood hazards. Both of these writers felt that burning impaired the vi-

tality of the chaparral, and consequently that it could be killed by repeated fires. Cooper (1922) followed these writers in believing that fire was destructive to a chaparral stand. He reasoned that the development and spread of chaparral was favored by protection from fire, and that therefore controlled periodic burning would tend to convert brushland to grassland. This view was also held by Bauer (1930).

Clements (1920) agreed with Leiberg (1900) and felt that extensive areas of sprouting chaparral were indicative of frequent fires. Jepson (1925) also pointed out that many chaparral species are favored by fire and increased in dominance where fires are frequent. Shantz (1947) emphasized the effect of fire, not only in maintaining a chaparral stand, but also in spreading brush species into other types of vegetation.

One of the earliest writers to be concerned with the succession occurring on burns in California chaparral was Brandegee (1891) who reported that abundant stands of certain species appear in burned areas and are not to be found in unburned chaparral. Cooper (1922) reported in considerable detail the vegetation succession observed on burns. He also distinguished primary succession—that occurring on bare rock surfaces —from secondary succession—that occurring after denudation by fire or other disturbance. Weaver and Clements (1929) discussed fully the difference between primary and secondary succession, and further, separated the chaparral subclimax (where brush has replaced a former timber stand) from the fire climax chaparral in southern California.

Fultz (1923) discussed in a popular vein the species comprising the chaparral formation, the succession occurring after fire, and the disastrous results of burning the vegetation on southern California watersheds.

The most important recent work on chaparral and its ecological aspects was that of Sampson (1944). This author described in detail the succsion occurring after burning chaparral in northern California.

The chaparral environment has been discussed in detail by Miller (1947) and Pequegnat (1951). The areas reported upon are similar to the Fern and Frankish Canyon study areas.

Effect of fires upon composition of the brush cover

The results of the present study substantiate the findings of Sampson (1944) that a sprouting chaparral cover can usually withstand repeated burning without loss of vitality. Even though many chamise plants in the study areas were killed by fire, there were always enough sprouting stumps and seedlings to perpetuate this species as a dominant. Sampson also stated that the nonsprouting species can be controlled by use of two fires spaced 2 years apart. The second fire kills most brush seedlings started after the first fire. The same result was brought about by a single spring fire at Barranca, where a fire in March of 1942 destroyed an existing ceanothus cover. Seedlings did not develop to replace the ceanothus. However, it should be stressed that the summer and fall fires in the study areas were followed by an increased number of ceanothus shrubs.

Development of temporary covers

A vigorous temporary cover developed on all study areas. Sampson (1944) reports a similar development of vigorous covers after burning of northern California chaparral, but the temporary covers in that region tended to be more dominated by annual grasses than were those in southern California. Another striking difference in northern California was the common occurrence of herbaceous plants in the chaparral before burning. These plants assured an abundant source of seed, and produced a vigorous cover quickly. On the study areas in southern California, herbaceous plants are very scarce in the mature chaparral, and are found only in the vicinity of rock outcrops, natural openings in the cover, and disturbed places such as road and trail sides. However, many species found nowhere in the old chaparral appeared abundantly after fire. Hence, the temporary cover in burns must have been produced either by invasion from the focal areas of pre-fire herbaceous plants or from viable seeds stored in the soil (more than 50 years at Fern Canyon!). Species of the latter group usually germinate promptly after fire. On the study areas these achieved dominance during the first several years. Those which invaded, notably the annual grasses, were often lacking in the first year but reached dominance later. Most of the temporary cover was completely eliminated in 10 years.

The deep soils produced the densest covers. At Barranca, these stands were composed primarily of annual herbs, but at Waterman, the perennial herb, *Penstemon spectabilis,* dominated the plots during the first years. The shallow soils usually produced a sparse cover, which was characteristically made up of numerous diminutive annual and perennial herbs. It is probable that weather conditions in the seasons following the fire and availability of seed are important factors in determining the kind of cover that develops.

A striking example of the variability of tem-

porary covers at the same location but under different conditions of burning and of weather after the fire, was afforded by the Barranca plots burned in the summer of 1925 and in the winter of 1942. Some of the dominants occurring after the first burning were insignificant in the cover after the second fire. Likewise, some species insignificant after the first fire became dominants after the second one.

Soil loss probably played a part in the development of temporary cover. For example, the Cholo Point plots, where erosion was severe, had a very sparse temporary cover in the first two postfire years. Very few perennial herbs appeared and the annual herbs (even such "fire-type" species as *Phacelia brachyloba* and *Lotus strigosus*) took two to three years to become abundant. The inference is that the seed supply was materially reduced by soil removal, and two or more years were necessary to build up a supply for production of the dense annual herb cover which the site could support. On other sites with less erosion, these "fire-type" species were most numerous the first season after the fire.

The temporary vegetation undoubtedly restrains erosion in burned areas. Although no measurements were obtained in the study areas to permit quantitative estimates of this effect, abundant evidence of it was observed. Most obvious, and most easily subject to photographic recording, were the numerous small litter-mats formed in inter-shrub spaces by fallen stems of plants such as *Stephanomeria* and *Dicentra*. The little terraces of wind- and water-borne soil impounded by these obstructions were commonly overgrown with annual plants, particularly *Bromus rubens* and *Phacelia brachyloba*, thus forming effective barriers to gully erosion between the shrubs (Figure 12). The extent of gullies that might have formed in the absence of these natural controls is, of course, not calculable. In the aggregate, however, the large number of these miniature check-dams per acre furnishes a considerable amount of soil stabilization on burned chaparral slopes.

. Fig. 12. Example of natural barriers to erosion formed in intershrub spaces by temporary vegetation in burned areas. In this case, the miniature check-dam was formed by fallen stems of *Stephanomeria* overgrown by *Bromus rubens*.

Long-time vegetation changes without fire

The discussion so far has outlined the vegetation changes in the first few years after fire. It is possible that as the post-burn vegetation matures, the conditions of microclimate and soil gradually change, in some places to such an extent that species which are characteristic of another type of vegetation might begin to gain a foothold. Sampson (1944) reported a definite trend toward grassland in northern California chamise-chaparral if protected from fire. Biswell and Street (1948) in central California reported increase of brush density in unburned mixed brush-grass stands, particularly where *Ceanothus cuneatus* (Hook.) Nutt. was present.

In the southern California study areas, neither of these trends was evident. Chamise appeared to be maintaining, and in many cases increasing, its dominance. Even in chamise-ceanothus chaparral there were no signs of chamise weakening or giving way to other species. Certain chamise shrubs were crowded by hoaryleaf ceanothus, but upon death of the ceanothus, the chamise individuals rapidly regained their vigor.

The only tendency toward change in vegetation type to be noted was the appearance of some oak chaparral or woodland species in the maturing chamise chaparral. In the 25-year-old cover at Barranca, many hoaryleaf ceanothus shrubs had died without replacement by seedlings. The resultant openings were occupied by a few annual herbs, notably *Ellisia chrysanthemifolia*, a common herb in the oak-woodland association. Also, a few seedlings of *Rhamnus crocea* var. *ilicifolia* and *Prunus ilicifolia* appeared; these species are more common in oak chaparral and woodland-chaparral associations.

Changes in cover density

When entire burned areas are considered, cover density generally increased steadily for some years after burning. On small plots within the larger area, the density usually decreased as the temporary cover died, and before the permanent cover showed much development. But because different species of the temporary cover reached dominance in differing lengths of time after the fire, each of these small areas experienced the decrease in density in different years.

However, a general decrease in cover density occurred later where relatively short-lived shrubs

were present in the stand. This occurred in the Barranca study area where the crown density reached a peak when the stand was about 17 years of age, and then started a slow decrease owing both to the gradual dying of the ceanothus and to the opening of the crowns of chamise. In the Fern Canyon study area, a decrease from the same cause was observed 14 years after the fire. In both areas these processes may have been speeded by the recent dry years.

Relation of results to management of brush areas

Information on plant succession after fire in the chaparral can be applied to advantage in the management of chaparral watersheds. Even though great effort is expended on fire prevention in southern California mountain watersheds, fires still occur and destroy the cover on large areas. As has been frequently reported, floods accompanied by severe erosion may occur from southern California watersheds denuded by fire (Kraebel 1934, Forest Service and Soil Conservation Service 1940, Adams, Ewing, and Huberty 1947, Kittredge 1948, Division of Forest Influences Research 1951). While the present study was not directly concerned with the problems of flood and erosion control, it has revealed information which bears upon the management of burned brush areas, or may aid in the conversion of brush to other plant types.

The study shows that summer and fall fires repeated at intervals of 12 years or more change a chamise-chaparral cover only temporarily. While the relative abundance of the several dominant shrubs may be changed by fire, the general type of shrub cover remains unchanged. In the first few years after a fire in chamise-chaparral, a temporary cover develops rapidly. This cover helps to stabilize the soil, but does not prevent the eventual formation of a normal brush cover.

In spite of the rapid regrowth of chaparral, severe erosion has often occurred from burned areas during the first several years after a fire. To reduce this soil loss, black mustard (*Brassica nigra*), commonly used as a cover crop in citrus groves in southern California, has frequently been sown upon burned areas in mountain watersheds there (Gleason 1948). The question has been raised whether a dense temporary cover such as is often produced by this species would have any influence upon the development of the permanent cover. Went, Juhren, and Juhren (1952) reported that mustard inhibited the development of native species such as black sage, laurel sumac (*Rhus laurina* Nutt.), and California buckwheat. Two other native chaparral species, hoaryleaf ceanothus and deerweed (*Lotus scoparius*), were not adversely affected. Their data, however, show that, even for the "inhibited" native species, sufficient individuals grew to perpetuate the stand in normal numbers. In the case of black sage, for example, a mean of 27 plants per square meter survived in the mustard-sown plot at the end of the second year. Observations in burned watersheds sown to mustard indicate that the growth of mustard does not prevent, either by inhibition or competition, the regrowth of a normal brush cover.

Replacement of the chaparral in southern California by coniferous plantations has been undertaken from time to time by individuals and public agencies for various reasons, the principal ones being to improve the watershed cover, and to increase the recreational possibilities. Plantations have often been started on burned areas, but the young introduced plants have usually been killed by competition with the vigorously regrowing chaparral. This is true even of Coulter pine (*P. coulteri* D. Don.) which grows naturally in parts of the chaparral zone. The scattered groves of planted conifers to be found today in the zone were especially favored because the roots of competing shrubs were dug from the sites before planting. The success of conifer planting in the chamise chaparral zone is not to be expected unless the shrub competition is eliminated.

Sampson (1944) concluded that, in northern California, fires two years apart will usually be effective in converting a non-sprouting chaparral to grass or herbaceous cover. No such closely spaced fires have been studied in southern California, but it is notable that a single fire, in March, 1942, at Barranca, eliminated hoaryleaf ceanothus from the cover. The reason for the failure of this species to reestablish itself in that burn is not clear, but several conjectures suggest possible explanations. The seed of this ceanothus normally ripens in June, and the likelihood that any seed could have ripened on the Barranca area before the March fire in 1942 is extremely remote. Seeds already in the ground from previous seasons might have germinated after the April rains of 1942, and the seedlings might have died before growing big enough to leave recognizable remains. Conditions for germination, other than the moisture requirement, might not have been right, either in April or later when the soil was moist. The seed of previous seasons might have been completely removed by rodents, birds or insects.[7]

[7] In June, 1932, at Barranca, when the ripe capsules of hoaryleaf ceanothus were popping their seeds, harvester ants were observed in the act of gathering every seed of this species on a 10-milacre area. The seeds were carried to nearby ant nests, "peeled" of their hard coats and fed to ant larvae underground. Where these ants are abundant it seems quite possible that an entire ceanothus seed crop could be consumed. However there is no evidence that ants were abundant in the Barranca area burned in March 1942.

spective of the reasons for the lack of seedling survival, the fact that hoaryleaf ceanothus did not reproduce itself after a March fire suggests the possibility that spring fires might accomplish the same results in some areas as the two closely spaced summer fires recommended by Sampson.

Acknowledgments

The authors wish to acknowledge their debt to the many persons who have contributed to this long-time project. The project was laid out in 1927 by C. J. Kraebel and R. B. Weaver with the advice of the late F. E. Clements and of A. W. Sampson. D. M. Ilch, C. H. Gleason, and J. S. Horton carried on the field work in later years with the help of various assistants. Most of the vegetation summaries were made under Horton's direction at the San Dimas Experimental Forest, Glendora, principally with the help of W. S. Dod, Works Progress Administration, and J. Gorman, R. R. Inglis, and S. R. Tyson, Civilian Public Service.

Summary

Development of vegetation after fire in the chamise chaparral of southern California was studied by means of periodic observations of permanently marked plots. The plots were located in chaparral dominated by chamise (*Adenostoma fasciculatum*) frequently associated with hoary ceanothus (*Ceanothus crassifolius*), black sage (*Salvia mellifera*), California sagebrush (*Artemisia californica*), chaparral whitethorn (*Ceanothus leucodermis*), Eastwood manzanita (*Arctostaphylos glandulosa*), and bigberry manzanita (*Arctostaphylos glauca*). The chamise chaparral was composed of species able to reproduce after fire. Two types of cover were recognized: the permanent shrub cover consisting of shrubs which made up the mature brush cover; and the temporary cover of annual herbs, perennial herbs, and short-lived subshrubs. Some species of the permanent cover, such as chamise, sprouted vigorously from the root crown after burning. Seedlings also developed from chamise seeds which germinated after the fire. Individuals of other species, such as hoaryleaf ceanothus were killed completely by fire, but many seedlings usually developed.

Composition of the permanent cover changed little after any of the burns. However, relative abundance of the several shrub species in the cover occasionally did change. For instance, the number of hoaryleaf ceanothus usually increased after summer and fall fires; but the species was practically eliminated after an early spring fire.

The temporary cover usually appeared and reached a peak of growth and density 2 to 5 years after the fire. Most species of this cover disappeared completely as the permanent cover matured. Seeds of these species apparently remained viable in the soil for long periods, *e.g.,* over 50 years in Fern Canyon. A few species reappeared sporadically in openings in the mature chaparral.

The composition of the permanent cover was largely determined in the first winter after a fire by the number of sprouting root crowns and the number of seedlings of permanent species. Conditions in the subsequent years were important in determining the number of surviving seedlings. Very few chaparral shrub seeds germinated after the first winter.

There were a few indications in this study of the development of true climax from the fire climax chaparral. Many individuals of *Ceanothus crassifolius* have died recently, thinning the permanent cover. A few seedlings of woodland chaparral species, *e.g., Prunus ilicifolia* and *Rhamnus crocea* var. *ilicifolia,* appeared on the plots after the fire type had reached maturity.

Cover densities increased rapidly to a maximum with the development of the temporary cover. A decrease in density sometimes occurred locally within a large burn owing to decline of the temporary cover before it was compensated for by growth of the permanent cover species. A second general decrease in density occurred in later years, particularly where one of the ceanothus species was important in the cover.

After removal of chaparral cover by fire, the exposed soil is subject to severe erosion. To combat the damages resulting from this soil loss, those concerned with management of these watershed areas desire to reestablish a plant cover quickly. This paper traces the development of the native vegetation and enables the watershed manager to fit his plans into the natural succession of vegetation.

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THE BIOLOGY OF THE GRAIN BEETLE *TENEBRIO MOLITOR* WITH PARTICULAR REFERENCE TO ITS BEHAVIOR[1]

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INTRODUCTION

The common grain beetle, *Tenebrio molitor* Linnaeus, is one of the "darkling beetles" belonging to the family Tenebrionidae. Species of the genus *Tenebrio* are black or dark in color, with moniliform antennae, with mouth parts somewhat reduced in size, and generally live in decaying forest vegetation. The usual food for most of the family is fungi. In its ecology, however, *Tenebrio molitor* differs considerably from most of the members of the family Tenebrionidae and from all but a few of the members of the genus *Tenebrio*. Of the four species of *Tenebrio* to be found in the Chicago area, two of them (*T. castaneus* Knoch. and *T tenebrioides* Beauv.) live in decaying logs and feed on fungi. The other two species (*T. molitor* L. and *T. obscurus* Fab.) are introduced forms and live in stored cereal or grain. The larvae of *Tenebrio molitor* are long and slender, having a general worm-like appearance. They are lighter in color than the adults and not as heavily sclerotized. Both the larvae and adults are detrimental to stored grains; neither, however, is injurious to the living crops.

It was the purpose of this investigation to reexplore and correlate some of the studies on the biology of *Tenebrio* previously reported, to examine in detail certain aspects in the biology of the animal not heretofore investigated, and to give particular attention to the behavior of the animal in response to various ecological factors, both physical and biotic.

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of Pennsylvania Hospital, for her skillful execution of the figures herein.

Eclosion

The process of eclosion, or emergence of the adult from the pupal case, presents a critical situation for *Tenebrio*. It is apparent from the number of "imperfect" eclosions that may be found in any culture of *Tenebrio* that some difficulty is frequently encountered by the animals during the process.

The entire process lasts approximately thirty minutes. The various steps occur in the following sequence: a. rhythic contractions of the tarsi; extension of the abdomen; b. violent contractions of the abdomen; asynchronous movement of the feet; c. alternate contraction and expansion of the abdominal segments; head and prothoracic legs free; anntenae and mouth parts move; d. mesothoracic legs free except for the tarsi; e. metathoracic legs free, except for the tarsi; f. metathoracic legs completely free; exuviae pushed clear; g. legs move in walking synchrony; animal rights self; after resting for a short period on its ventral surface, the beetle stands up on its legs and begins to walk.

Effects of Molds

Although it has not been found that the molds have any lethal effects on *Tenebrio* ("accidental" laboratory molds, of the order Moniliales in the Fungi Imperfecti), it was found that the animals reared in moldy culture medium had a pronounced reduction in size. There was no evidence that the mold retarded the rate of development. It was observed that the time of eclosion in the "mold" group was precisely the same as that in the normal cultures. In both groups, eclosion occurred on the ninth day after pupation.

Records were kept for five animals which pupated on the same day in the moldy culture, and for five which pupated in normal cultures. The average daily weights of the pupae in the moldy culture dropped from 84 mg. on the day of pupation to 77.8 mg. on the day before eclosion. The corresponding values for the normals were 157.3 mg. and 148.3 mg., respectively. As adults, those reared in the moldy culture dropped in weight from 69.0 mg. on the first day after eclosion to 43.0 mg. on the 21st day. The corresponding values for those reared in normal cultures were 132.3 mg. and 93.0 mg., respectively. It is probable that the mold rendered the food distasteful to the larvae, thus limiting their feeding, which would in turn produce smaller pupae and smaller adults.

Commensalism

In the cultures of *Tenebrio molitor* there are several other organisms that may live with this species in a rather loose commensal relationship. Usually these commensals are of little consequence, unless their reproductive potentials are such that they can crowd out *Tenebrio,* a phenomenon which has been shown with two species of flour beetles (Park 1948). But occasionally there will occur a tremendous number of one of the commensal species which is detrimental to the populations of *Tenebrio.*

The most common commensals in a *Tenebrio* culture are the flour beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst, the flour moth *Ephestia kuhniella* Zeller and various mites of the family Acaridae. Although no actual tests have been made of the population dynamics among these three groups of organisms, several gross features are apparent. *Ephestia* has never been seen in the cultures used as stock for these experiments and observations in numbers large enough to suggest that *Tenebrio* populations were in any danger of being crowded out. On the other hand, one culture with only a few *Tribolium confusum* initially present changed during a period of six months to an almost exclusively *Tribolium* population.

The mites show the most dramatic fluctuations in their populations. During a period of two years, in February of each year, the mite populations suddenly increased so that the sides of each culture container were coated with mites. Close inspection revealed them on every flake of cereal examined. They were also all over the adults, pupae, and larvae, but there was no indication of parasitism. The mites feed on the cereal. In addition, however, when one of the beetles is injured, the open wound seems invariably to be covered over completely with mites. The numbers of mites increase to enormous proportions during the month of February, than drop with about the same rapidity. Although they might inhabit any of the containers of cereal, the mites are always most numerous in the containers with the most mold. These containers are also the most moist.

There are several mites of the genus *Acarus* which inhabit cereals. One of the most common of these is the grain-flour mite, *Acarus siro* (L.). This mite appears to fall into the category of "incompletely overlapping generations" described by Davidson (1944). Shortly after the periods of maximum numbers, the adults disappear completely, leaving only immatures in the cultures. Population increases of this sort have been shown

by Ford (1937) with Collembola and mites living in grass. When such cycles occur in nature, in temperate regions, the phenomenon is regarded as an adaptive response to the rigors of winter climates (Allee *et al.* 1949). But the precise significance of such cycles in grains stored indoors remains a question.

Light and Chemical Experiments

Materials and Methods. In the light and chemical experiments, the animals were kept in individual petri dishes. In the first series, testing for the orientation to lateral daylight, the larvae were kept and tested in covered petri dishes 7 cm. in diameter. The background under the dishes was white. The dishes were arranged in a row two feet from the window. There were five larvae in each dish, with three dishes each of five larval sizes. Readings were taken at various times during the day. The basis for the reading was the percentage of animals in each dish found on the side of the dish away from the light. The dishes were marked into halves, and any animal on the line between the two halves was scored as 50% away from the light. A corresponding series of animals was kept in the dark and removed briefly for the reading.

In the light-dark experiments, "alternative chambers" were used. These consisted of 9 cm. petri dishes which were transparent on one half and painted black on the other. Each dish had a dry filter paper on the bottom to facilitate the movement of the animals. The light source was an Erb and Gray lamp. The light readings taken showed an intensity of 600 foot candles in the center of the chamber, and 500 foot candles around the periphery. The animals were subjected to both two- and five-minute tests, being kept in the dark when not being tested. A stop watch was used for the timing and the times noted each time the animal being tested left one area and entered the other. From these data, the precentage of time the animal spent in the dark was calculated and recorded as the index of the animal's degree of photonegativity for that test. After several tests had been run, decided variations appeared in the results of the various groups because of the inactivity of individual animals in certain groups. For this reason, calculations were made involving only the active animals on one hand, and the total group on the other.

In the chemical experiments, the insect repellent paradichlorobenzene (PDB) was used. In one series of tests, the PDB was put in the dark part of the alternative chamber. In another group, the PDB was put in one half of the dish all of which was illuminated, and the avoidance of the PDB by the insect was calculated in the same manner as its avoidance of the dark in the preceding experiments. The tests in this series were run in the same manner as the light-dark series, both adults and larvae being used, and both two- and five-minute tests being run.

Results and Observations. In the first series of experiments, using 75 larvae (15 of each of five sizes), it was found that the animals exposed to lateral daylight illumination selected the side of the dish away from the source of light 65.26% of the time, as contrasted with the essentially random distribution of those kept in the dark, which were found on the corresponding side of the dish in only 53.03% of the time (Fig. 1). This agrees with the findings of Brandt (1934) in his work on the larvae of the grain moth *Ephestia kuhniella.*

In the second series of experiments, 20 larvae were tested for their behavior in an alternative chamber, the alternatives being light and darkened areas. In these 5-minute tests, a wide divergence in the results from considering actives alone and total numbers of animals is apparent. Whereas the actives spent 81.4% of the time in the dark, the entire group (inactives plus actives) averaged only 69.9% (Fig. 2). The animals were intro-

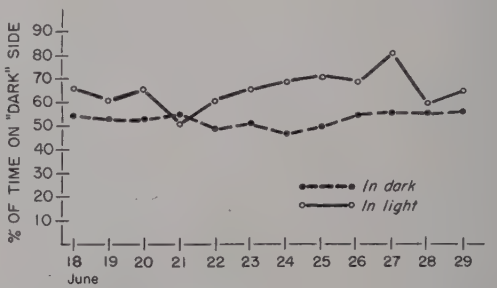

Fig. 1. Orientations of larvae of *Tenebrio molitor* to lateral daylight.

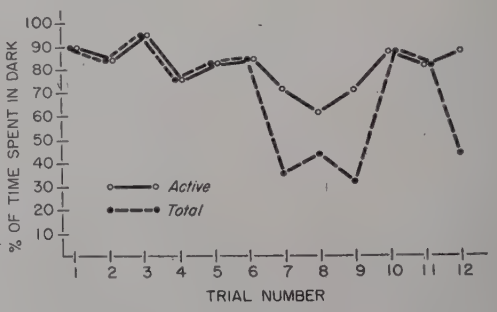

Fig. 2. Reactions of larvae to overhead illumination in alternative chamber (5 min. tests).

duced into the light area in each case, and the inactives were either too slow in moving to reach the dark area, or did not move at all. With these considerations, it seems probable than an evaluation of the actives alone would give a more characteristic picture of the behavior of the organism under these experimental conditions. (This view will be supported later in a consideration of the effect of approaching pupation on larval activity.)

In the third series, 20 larvae were tested as above, but for two minutes only per test. The results of these tests are shown in Figure 3. It

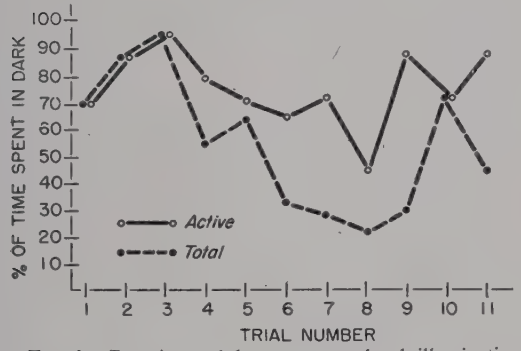

FIG. 3. Reactions of larvae to overhead illumination in alternative chamber (2 min. tests).

appears that both the actives and the "totals" spent a smaller percentage of the time in the dark than in the previous tests. This might be attributable to the fact that the animals were introduced into the illuminated area, an appreciable amount of time being spent getting to the dark side.

In the fourth series of tests, adult beetles were given two-minute trials in the light-dark alternative chamber. The results (Fig. 4) show again

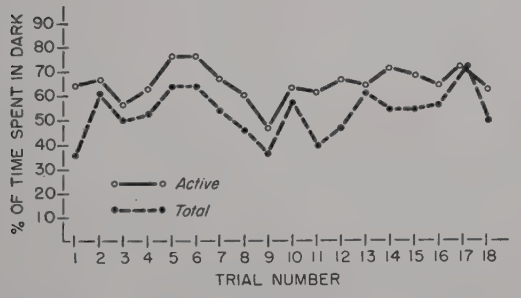

FIG. 4. Reactions of adults to overhead illumination in alternative chamber (2 min. tests).

the value of considering the active animals alone, for the *total* readings on the two series are about the same (54.83% for the larvae and 53.16% for the adults). The apparently lower photonegativity of the adults was demonstrated by their venturing back into the light from the darkened area with little or no hesitation, whereas the larvae demonstrated a tendency to remain in the dark once they had reached that area.

In the fifth series of experiments, the same apparatus was used as in the light experiments, except that the chemical paradichlorobenzene was sprinkled around the dark area. One gram of it was used, which gave a fairly uniform covering for that half of the dish. A parallel series was conducted with conditions the same, except that there was no darkened area in the dish. This was designed to show the reactions of the animals to the chemical alone. In both of these series, 20 larvae were used and each test ran for five minutes. The results (Fig. 5) show the differences

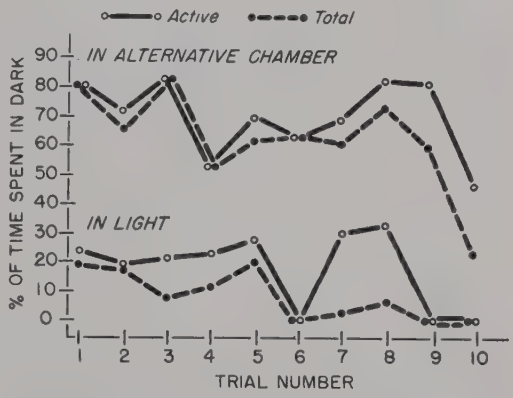

FIG. 5. Reactions of larvae to PDB in light and in alternative chamber of light and dark (5 minute tests).

in the behavior of the larvae under these two sets of conditions. The figures would be even more dramatically contrasted if the readings for the last two days were not included. The lower readings in both the "PDB" and "no PDB" groups on the last days of the experiments were attributable to pupation two days after the last reading. Comparison of the two major groups in Figure 4 gives a convincing picture of the strong negativity of the animal to light. When a darkened area was not available (Fig. 5), the animals spent an average of only 17.81% of the time in the PDB area, but when they had an alternative of PDB with darkness, or light without PDB, they selected the former 69.84% of the time (actives). This suggests that the reaction of the larvae to light is more strongly negative than to the insecticide paradichlorobenzene.

The sixth series of tests was similar to the above, except that the time of the tests was limited to two minutes. The results (Fig. 6) are not

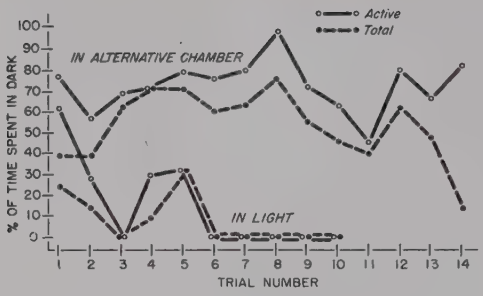

FIG. 6. Reactions of larvae to PDB in light and in alternative chamber of light and dark (2 minute tests).

essentially different from those obtained in the five-minute tests.

The seventh series of experiments was similar to the sixth, except that adults were used instead of larvae, and 40 animals were used in both the light-dark and all-light groups. Again, as in the "light" experiments, the adults spent less time in the darkened area than did the larvae (in the preceding series). This can be seen in a comparison of Figure 7 and Figure 6. Further, it can be seen in a comparison of Figure 7 and Figure 4 that the adults spend less of their time in the dark when PDB has been added to that area than when PDB was not present. It may also be noted that the adults spend almost twice the amount of time in the area of PDB if it is darkened, than they do when it is not. Again, as with the larvae in the preceding experiments, the negativity of the adults to light appears stronger than their negativity to the insecticide.

In these and other studies of the behavior of the larvae of *Tenebrio molitor*, a conspicuous difference is immediately evident in the behavior of the individual animals. Some are very active, others quite inactive, despite the uniformity of conditions to which they were subjected. For this reason, the activity of larvae immediately prior to pupation was analyzed. Although the records of only five individuals were available, there is sufficient evidence presented in them to draw conclusions concerning the effect of approaching pupation upon larval activity (Fig. 8). The gradual decrease in activity of the larvae is evident, starting about one week before pupation. It is this effect which interferes frequently with the various behavior experiments undertaken with *Tenebrio* larvae.

Discussion. A correlation of the foregoing experiments of the "light-dark" and "chemical" series reeveals several basic features about the behavior and orientation of *Tenebrio molitor*. First, it is shown that the larvae exhibit a stronger (negative) orientation to light when given an alternative between light and dark than in a gradient of decreasing light intensity provided by "lateral daylight" (Figs. 1-3). A correlation of all the light and chemical experiments using overhead illumination is given in Table I. From these data, it would seem at first (first and second columns) that both larvae and adults show sensitivities to light and to PDB which are approximately equal, the larvae avoiding light and PDB

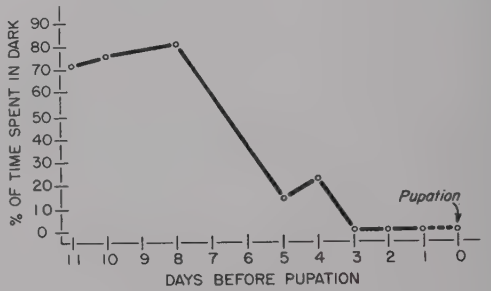

FIG. 8, Effect of onset of pupation on larval activity.

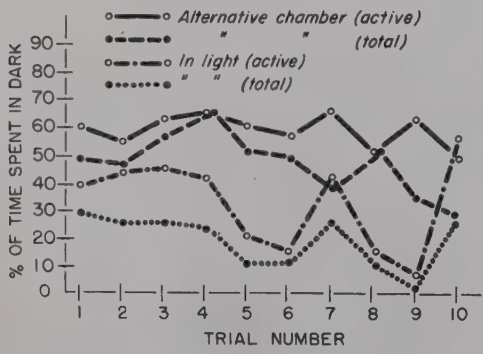

FIG. 7. Reactions of adults to PDB in light and in alternative chamber of light and dark (2 minute tests).

TABLE I. *Summary of Light and Chemical Experiments*

	Per Cent of Animals on "Test Side" of Dish		
	Light-Dark	Light-PDB	Light—Dark+PDB
	Larvae - 5-Minute Tests		
Actives.....	81.42± 9.45	17.81±13.00	69.84±12.67
Total.....	69.88±23.56	8.61± 8.21	62.32±16.68
	Larvae - 2-Minute Tests		
Actives.....	75.92±14.39	15.26±23.10	73.25±12.80
Total.....	54.83±28.29	8.16±12.11	54.09±17.11
	Adults - 2-Minute Tests		
Actives.....	64.99± 6.81	33.11±16.68	58.60± 5.64
Total.....	53.16± 9.87	19.90± 9.65	47.06±10.71

81% and 82% of the time respectively in five-minute tests, whereas the adults avoided light and PDB 65% and 67% of the time respectively in two-minute tests. But the third column shows clearly that both the larvae and adults are more strongly negative to light than to the insecticide PDB, for when given the alternative of "light without PDB" or "dark with PDB", both groups selected the latter most of the time. It is apparent that the larvae are more sensitive than the adults, both to light and to PDB. Further, it appears that the larvae, though more sensitive to PDB than the adults, will select the area with the chemical in it, if that area is darkened (and the alternative area is not) because of their marked photonegativity.

Humidity Reactions

A series of tests was conducted with ten adults to ascertain tendencies to aggregate with differential humidities. A black covered evaporating dish (24 cm. in diameter and 8 cm. deep) was the test chamber. The bottom was covered with filter paper to provide a suitable walking surface. Cardboard "sheds" were used for aggregation chambers, each 5 cm. long, 5 cm. wide, and bent down the center at a 90° angle.

A series of five tests was made to ascertain the aggregating tendency of the animals under moist sheds in the dark, with no other moisture available than that in the air. The test chamber was divided into three equal parts, each separated by lines joining at the center at a 120° angle. Over each of these lines, halfway between the center and the periphery, in an orientation parallel to that of the line, a wet shed was placed. Ten animals were introduced into the chamber, and kept in the dark for a period of two hours or more (from 2 to 24 hours). In none of the tests was aggregation noted; rather, random distribution was the order.

In the second series of tests, the same animals were given an alternative of wet or dry sheds. Six sheds were used, alternating wet and dry, being oriented as before, but with six in the circle instead of three. In the five tests made, a total of 16 animals came to rest under the dry sheds, while only 7 were found under the wet sheds. This represents a total of fewer than half of the animals used in the tests, which suggests that under dark conditions, there is little response to higher humidity.

In the third series of tests, the animals were subjected to overhead illumination (100-Watt bulb, one foot over the center of the dish), and given access to three wet sheds. The time was recorded for total aggregation in a ten-minute period. As each beetle entered a shed, the time was noted so that each test had a numerical time rating for the "entrance of the first beetle into a shed", etc. From these notations, the average times for the entrance of each into the sheds were calculated. At the end of each test, the number of beetles in each shed was noted. On the average, the first beetle entering a shed was timed at 9.1 secs., the eighth to enter averaging 292.9 secs. In only one test did a ninth beetle enter a shed in less than ten minutes, that time being 530 secs. In no case did a tenth beetle enter a shed in less than ten minutes. The maximum number of beetles found in any one shed in any of the tests was four, and this number in no case represented more than half the total number under all the sheds at the end of the test. Furthermore, since none of the beetles *ever* left a shed, once it had entered it, it is suggested that the photonegativity of *Tenebrio molitor* is stronger than its aggregating tendency in governing the orientation of the animal.

In the fourth series of tests, the conditions were the same as in the third series, except that the sheds offered were dry. In these tests, the first beetle entered a shed on an average of 55 secs., the sixth averaged 525 secs., and in no case did more than six beetles enter a shed. It is apparent from these results that the light avoidance is much less pronounced when moisture in the darkened area is at a minimum. It is possible that the moisture in the former test acted as a stimulus complementary to the inherent photonegativity of the animal.

The results of the third and fourth series of tests are shown in Figure 9. The results of each test with the wet sheds were so irregular that each was plotted separately, then the "average

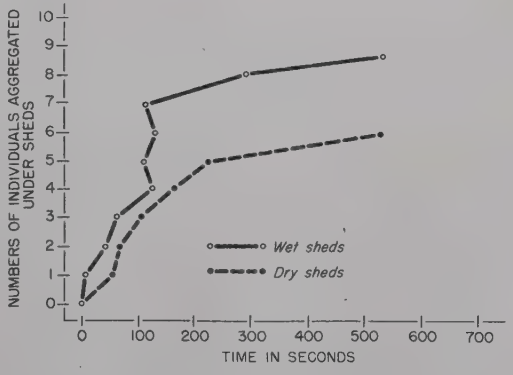

Fig. 9. Aggregations of adults under wet and dry sheds.

curve" was superimposed on these individual curves. The "average curves" (for both the third and fourth series) are shown in Figure 9.

The less complete aggregations among the "dry" tests might be interpreted as an evidence that *Tenebrio* follows the land isopod tendency to wander about and increase its locomotor activity under conditions of reduced humidity (Allee 1926).

Letisimulation

The phenomenon of letisimulation, or catalepsy, is widespread in the animal kingdom, both among the vertebrates and the invertebrates. Letisimulation is the act of death feigning when disturbed. Its occurrence in the Virginia opossum is common knowledge. Among the reptiles, the hog-nose snake, *Heterodon,* is notable for this behavior (see an unpublished Ph.D. dissertation at Northwestern University, 1952, by R. A. Edgren). Among the insects, letisimulation has been studied in several families of beetles. Abshagen (1941) found that sudden shadowing had a greater effect in eliciting a letisimulative response than did sudden illumination. Weiss (1951) found that the duration of the letisimulative period varies with the force of the stimulus and inversely with the temperature.

Observations of letisimulation were made with *Tenebrio* at first only incidentally to various other behavior studies. But the seeming regularity of its occurrence stimulated a series of tests for letisimulation alone. It was at first observed that when an adult *Tenebrio* was handled, frequently it would not run away, but remain motionless on the spot where it was released. The duration of a letisimulative period varies greatly.

The beetles were introduecd into petri dishes 9 cm. in diameter, one at a time. The stimulus used was that of handling the beetle with forceps. If the beetle being tested did not letisimulate immediately, it was scored as "0". If it did letisimulate, the period of letisimulation was timed, the maximum duration of any test being three minutes. Although letisimulation was not the usual response, it did occur with appreciable regularity. Also, when it did occur, it was usually for a more or less extended period of time. In 19 of the 80 tests made, letisimulation was shown. Of these beetles that letisimulated, the average period of letisimulation was 63.84 seconds. The total average letisimulation decreased from 29.3 seconds on the first trial of the 16 beetles used to 0 on the fifth trial.

Although the data on letisimulation are admittedly few, it was noted that there is a tendency for the length of the letisimulative period and for the frequency of occurrence of the act to diminish with consecutive tests. This is in accord with the findings of Weiss (1951) on the scarabaeid beetle *Diplotaxis liberta.* This suggests that the response is capable of being conditioned. It is interesting to note that this same pattern of acclimation to unfamiliar circumstances can be discerned in the species response to light intensity and to poisonous chemicals.

In contrast to this relatively regular occurrence of letisimulation in the adult beetles, neither the larvae nor the pupae show any such behavior. The larvae move rapidly away when released after handling, and move constantly while being handled. The pupae, though incapable of locomotion, exhibit violent movement in the form of dorso-ventral thrashing movements of the abdomen.

General Discussion

Since a discussion was given previously in each major section, only a few general remarks will be given at this point. Observations on the effects of molds showed the drastic effects molds have in limiting the size of *Tenebrio* pupae and adults. In its normal environment of stored grains, it would appear that individuals living in moist (and moldy) cereals would be likely to be unsuccessful in competition against those living in dry grains, because of the smaller size of the former.

The pronounced photonegativity of both the larvae and the adults (actives) of *Tenebrio* is consistent with the normal activities of the species. Some individuals may spend their entire lives without being exposed to light.

The humidity reactions of *Tenebrio molitor* present an interesting complex. In complete darkness, the animals show no selection of the moist areas, but when given the same alternatives in the light, the animals aggregate in the moist dark areas much more rapidly than in the dry dark areas. It has been demonstrated (Gunn and Pielou 1940) that *Tenebrio* is more active at the upper end of the humidity gradient. The relations of these reactions to the normal activities of the animal present a problem. If the animal be attracted to a higher humidity, it would be likely to find itself in moldy grain, the detrimental effects of which have been shown above. It seems probable that the strongest reaction of the animal is away from light. If it finds itself in a humid environment, its activity is maintained at a relatively high level until a drier area is found. In these drier areas, it is known that tenebrionid beetles can survive more easily than most of their com-

petitors, and here conditions are optimal for their nutrition and reproduction.

Summary

1. The effects of mold in the cultures of *Tenebrio molitor* on pupal and adult weights are given, and these weights are compared with weights of pupal and adult beetles reared in normal cultures without mold.

2. The results of a few observations are given of the interactions among the several grain inhabitants that may occur with *Tenebrio molitor*: the flour beetles of the genus *Tribolium*, the flour moth *Ephestia*, and mites of the genus *Acarus*. Of these, *Tribolium* appears to be more detrimental to populations of *Tenebrio*, but the mites show the greatest fluctuations in population density.

3. Analyses of the reactions of *Tenebrio* larvae and adults to various conditions of light, dark, and the presence of the insecticide paradichlorobenzene (PDB) are given. Various combinations of these conditions indicate that the apparently inherent photonegativity of the species is a stronger directing force in the behavior and orientation of *Tenebrio* than is its negativity to the lethal chemical PDB.

4. Humidity experiments showed that the animal does not usually aggregate in the dark, but under various conditions of light, dark, moisture and dryness, aggregations were seen to form as negative responses.

5. Observations of the widespread phenomenon of letisimulation (death feigning) are described. The adults are more inclined to exhibit this behavior than are the larvae or pupae.

6. The tendency of *Tenebrio* to acclimate to unnatural circumstances has been described. This was shown in the responses to light intensity, poisonous chemicals, and mechanical stimulation by handling.

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CHARACTERISTICS OF THE *STIPA COMATA-BOUTELOUA GRACILIS-BOUTELOUA CURTIPENDULA* ASSOCIATION IN NORTHERN COLORADO

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Introduction

The vegetation of the mountain-front zone of northern Colorado consists of zonations and mosaics of stands of several kinds, chiefly grassland and shrub. The chief kinds of grassland communities are the *Stipa comata-Bouteloua gracilis-B. curtipendula, Andropogon scoparius, Agropyron smithii-Bouteloua gracilis-Bromus tectorum, Bouteloua gracilis-Artemisia glauca, Stipa viridula,* and *Andropogon gerardi.* The chief shrub community is *Cercocarpus montanus,* occurring on more rocky sites and usually higher on the slopes than the grasslands. Other shrub communities are the *Physocarpus monogynus* on some northerly slopes, *Rhus trilobata* in various sites, and in valleys, *Symphoricarpos* spp., *Prunus* spp.,

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FIG. 1. Stand F4 on Morrison limestone. Scattered shrubs are *Cercocarpus montanus* and an occasional *Rhus trilobata*. Chief grass is *Stipa comata*. *Pinus ponderosa-Cercocarpus montanus* stand on outcrop of Dakota sandstone in right background. July 14, 1953.

Ribes spp., and others. *Pinus ponderosa* is often scattered among the shrubs, especially *Cercocarpus*, on rocky outcrops, particularly those of the Dakota Formation (Fig. 1).

The aim of the present study is to describe characteristics of the *Stipa comata-Bouteloua gracilis-B. curtipendula* community on the basis chiefly of eight distinct stands within an area of about 1 by 2.5 miles in the lower foothill region between Big Thompson and Little Thompson canyons, mostly in R. 70 W, T. 4 N. The elevations of these stands was between 5,300 and 5,600 feet. The soils were derived from various geological formations, chiefly Morrison limestone (Jurassic) and Dakota sandstone (Cretaceous), but stands also occurred on Lykins sandstone (Permian-Triassic), Lyons sandstone (Permian), and Niobrara limestone (Cretaceous). The field work was done during July, 1953.

The stand is the basic unit of vegetation. It forms the ideal starting point in a study of the vegetation of an area. Knowledge of individual stands is essential for the classification of stands into communities, characterization of communities, for the study of causes of differentiation of vegetation into communities, and for research in community-environment and plant-animal relationships. Intensive research is usually conducted within a restricted area, at times within a single stand, so that error caused by variation in vegetation and soil will be reduced to a minimum. It is desirable that the stand which is selected should be as typical as possible of the kind of community under investigation. Preliminary field examination indicated that the *Stipa comata-Bouteloua gracilis-B. curtipendula* stands were well-suited to a comparative study because of their distinctive physiognomy, usually sharp differentiation from surrounding types, and their frequent occurrence. It appeared difficult, if not impossible, to select by observation a stand which would best represent this type of community for intensive research. Quantitative analysis of the composition of the vegetation appeared necessary for this purpose so that the stands could be fully compared. This analysis was also necessary to determine the most typical and limiting characteristics of this kind of community. Stands of other kinds of communities were also analyzed for comparison.

General features of the vegetation, geology, topography, soils, and climate of this region have been summarized by Vestal (1914, 1917, 1919) so they will not be discussed here except to give a brief account of climatic conditions. The mountain-front zone is located in the semiarid climatic type of Thornthwaite (1948). The annual march of mean temperature (48-year record), precipitation (58 years), and snowfall (26 years) at Waterdale (40° 25′ N., 105° 12′ W.), at an elevation of 5,200 feet and about 5 miles north of the nearest stands, are as follows:

	J	F	M	A	M	J	J	A	S	O	N	D
°F.	27.2	30.2	37.2	46.7	54.6	63.3	69.1	68.1	60.3	49.3	38.1	29.8
ppt. (inches)	0.32	0.60	1.20	2.21	2.66	1.86	1.86	1.45	1.44	1.22	0.44	0.51
snow (inches)	4.0	9.8	11.1	5.5	0.6	0.0	0.0	0.0	0.1	2.7	5.6	7.5

The mean annual temperature is 47.9°F., the lowest on record —41° F., the highest, 102° F. The mean annual precipitation is 15.87 inches, varying over a 36-year period from 9.09 to 27.95 inches. The average annual snowfall is 46.9 inches. In a 39-year period, the greatest precipitation in 24 hours was 3.54 inches. The number of days with 0.01 inch or more of precipitation per day averaged 65, the largest per month, 9, occurring in July. The average number of days without freezing temperatures is 141, the earliest date of freezing temperature on September 9, the last in spring as late as June 3 (U. S. Weather Bureau).

Retzer (1953) pointed out that the important features of soils in the foothills are soil texture, thickness of soil over the bedrock or impervious layers, fertility, and erodibility or stability. He stated that in the Rocky Mountain region the first criterion to use in looking for differences in soil is the type of parent rock. Steepness of slope is also important. Differences in soil conditions may be recognized by differences in the kind or abundance of species and the vigor of growth unless

there is a masking effect caused by other influences such as grazing. One of the most critical factors influencing the composition of the vegetation in the mountain-front zone appears to be the depth and duration of available soil moisture (Hanson, *et al.* 1931). Variations may often occur within a small area, forming microhabitats. They are caused by topography, differences in soil texture, variations in the kind and extent of rock or organic material in the surface soil, animal activities, and atmospheric conditions, particularly the drying effects of wind and sun. If these variations in environmental conditions and in the vegetation are so pronounced that the vegetation type in each microhabitat is highly distinctive, then the vegetation can be considered a mosaic. Although there was variation in microhabitats in the stands selected for study, the variation in the vegetation was not great enough to make a mosaic (Hanson 1950: 285).

Stands for detailed analysis were selected on the basis of their apparent homogeneity as indicated by the physiognomy, kinds and distribution of prominent species, and by the uniformity of the site. Only stands of ample size, in good to excellent condition in vigor and composition, free from effects of excessive erosion or severe grazing, were used. Marginal portions were not used.

To secure data on the kinds, herbage cover, and the distribution of species 10 or 20 one-meter^2 quadrats were systematically distributed within each stand, usually along parallel lines several meters apart extending along the contour of the slope. The quadrats were placed at definite intervals, from 30 to 60 feet apart depending upon the area of the stand. The herbage cover was estimated according to the modified Hult-Sernander scale (Hanson 1953), as follows: 1 denotes herbage cover of less than 1/16 of the quadrat, 2—1/16 to 1/8, 3—1/8 to 1/4, 4—1/4 to 1/2, 5—1/2 to 3/4, and 6—3/4 to 4/4. The average cover and frequency of each species were calculated, and the summarized results are presented in Table I. This association table and the tables of individual stands have been indispensable in analyzing the vegetation (Braun-Blanquet 1950, 1951).

In each stand, a spot was carefully selected for digging a pit to describe the soil profile and for taking samples for laboratory analysis. The spot was located in vegetation that was as typical as possible of kinds of species, cover, and height of the plants. This was done after the vegetation had been analyzed so that advantage could be taken of the tabulated data and a "feel" for the stand had been gained. The colors of the dry soil were described according to the Munsell notation of color (Soil Survey Staff 1951). Soil samples from 0-6-inch depth, 6-12 inches, and 12-18 inches were tested in the laboratory for lime content (degree of effervescence with 20 per cent HCl), soil reaction, percentage of gravel, and percentages of sand, silt, and clay in the gravel-free portion. The indicators used for determining the pH values were chlorphenol red for pH 5.2 to 6.8, bromthymol blue for pH 6.0 to 7.6, and phenol red for pH 6.8 to 8.4. The gravel content was taken as the material that did not pass through a 2-mm. sieve, after the coarse rocks had been eliminated. The sand, silt, and clay percentages were determined by the most recent Bouyoucos hydrometer method (Bouyoucos 1951).

In analyzing the data on the vegetation, the association table, the species number-area curve, frequency class polygons, and Sörensen's coefficient of similarity (Sörensen 1948) were found helpful (Braun-Blanquet 1950, 1951; Nordhagen 1943).

Description of Stands

Stand F1, consisting of about 2 acres, was located on the upper part of an east-facing slope of about 15° on a ridge of Morrison limestone. The elevation was about 5,600 feet. Numerous rocks, often coated with lime on the lower parts, were scattered over the surface. The uppermost inch of soil was loose, consisting of fine granules and intermixed stones, pebbles, and plant debris. Between 1 and 8 inches, the soil was hard and compact, with aggregates up to an inch across. The color changed from very dark gray brown near the surface to brown at 12 inches. Rocks and gravel were scattered throughout the clay loam soil to 18 inches, but were most numerous in the upper foot. The gravel content decreased sharply from 20.5 per cent at 0-6 inches to 10.5 per cent at 6-12 inches and 9.6 per cent at 12-18 inches (Table IV). The sand content also decreased with depth, but the silt and clay contents increased, the clay reaching 40.6 per cent at 12-18 inches. The soil reaction was moderately alkaline, pH 7.6 to 8.0, and the lime content was very high as indicated by the very strong effervescence with 20 per cent HCl and by the lime flecks which were especially numerous below 12 inches. The vegetation was uniform in appearance because of the high frequency and cover of *Stipa comata*. *Bouteloua gracilis* and *B. curtipendula* together formed a lower layer, but, in quadrats where *B. gracilis* had a high percentage of cover, *B. curtipendula* had a low percentage, and vice versa. Other grasses and forbs were poorly represented. The average number of species per quadrat was

TABLE I. *Stipa comata-Bouteloua gracilis-Bouteloua curtipendula association*
(C=cover; F=frequency percentage)

Analysis number	F1		F2		F4		F6		F8		F9		F7		F5		Ave. cover	Ave. frequency %	Constancy %
Date, 1953	7-6		7-6		7-14		7-17		7-23		7-23		7-21		7-17				
Number of m² sample areas	10		20		20		20		10		10		10		20				
Slope; direction, degrees	E 15		W 30		ESE 5-10		E 15		W 25		W 10-15		W 10-15		W 10-15				
Total number of species	23		36		40		43		41		40		41		49				
Ave. no. species per m²	8.3		10.4		11.5		13.0		12.3		11.3		15.5		13.2				
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F			
Agropyron griffithsii			0.4	25			0.9	50	0.1	10			0.2	20	0.3	15	0.4	15	62.5
Agropyron smithii	0.3	40					0.4	30	0.1	10	0.1	10	0.3	30			0.2	15	62.5
Andropogon gerardi					0.1	50	0.4	30					0.7	50	1.4	55	0.6	23	50.0
Andropogon scoparius			0.2	15	0.4	20	0.3	20			0.2	20	0.7	40	0.8	40	0.4	22	75.0
Aristida longiseta	0.5	40	0.5	35	0.4	40	0.9	80	0.3	30	0.3	30	1.2	90	1.9	95	0.6	55	100.0
Bouteloua curtipendula	1.9	90	2.0	100	1.8	100	2.2	100	1.7	100	0.8	60	1.4	100	1.9	90	1.7	92	100.0
Bouteloua gracilis	1.9	80	0.8	50	1.4	60	0.8	45	1.4	90	2.2	90	1.8	80	2.4	90	1.6	73	100.0
Bouteloua hirsuta													0.1	10			0.1	1	12.5
Bromus japonicus	0.6	100	0.7	100	1.0	90	1.0	100	1.0	100	0.6	70	1.0	100	1.1	100	1.0	95	100.0
Bromus tectorum							0.1	10	0.2	20			0.1	10			0.1	5	35.7
Buchloe dactyloides											0.1	10	0.2	10			0.1	2	25.0
Carex heliophila													0.7	70	0.2	15	0.4	12	25.0
Festuca octoflora											x	10	x	10	x	10	x	4	37.5
Koeleria cristata							0.3	25			0.1	10	1.6	100	0.4	40	0.6	22	50.0
Sitanion hystrix	0.3	40	1.0	90	0.9	90	0.2	20	0.5	50	0.3	30	0.1	10	0.3	25	0.4	44	100.0
Sporobolus cryptandrus											0.1	10					0.1	1	12.5
Stipa comata	4.3	100	3.7	100	4.0	100	1.8	100	2.7	100	2.6	100	1.0	90	1.5	100	2.7	99	100.0
Allium geyeri					0.1	25					x	10			x	5	0.1	5	37.5
Ambrosia psilostachya									0.1	10	0.1	10					0.1	2	25.0
Artemisia frigida			0.3	30	0.6	55	0.6	45	0.3	30	0.5	40	0.9	80	1.1	75	0.6	44	87.5
Artemisia glauca	0.2	20			0.1	5			0.1	10	0.3	30	0.4	40	0.1	5	0.2	14	75.0
Artemisia ludoviciana			0.1	10			0.8	65	0.2	20	0.1	10	0.6	60	0.3	25	0.3	24	75.0
Asclepias hallii											0.1	10			0.1	5	0.1	2	25.0
Asclepias pumila			0.1	5													0.1	1	12.5
Aster commutatus crassulus					0.1	5	0.2	15					0.2	20			0.2	5	37.5
Astragalus drummondii			0.4	30													0.4	4	12.5
Astragalus flexuosus	0.2	20			0.2	20					0.1	10					0.2	6	37.5
Astragalus sericoleucus					0.1	5									0.1	5	0.1	1	25.0
Astragalus shortianus					0.1	5			0.2	20					0.1	5	0.1	4	37.5
Camelina microcarpa									x	10							x	1	12.5
Castilleja sessiliflora					0.1	5											0.1	1	12.5
Chenopodium pratericola	x	10															x	1	12.5
Chrysopsis villosa									0.1	10					0.1	5	0.1	2	25.0
Comandra pallida															0.3	20	0.3	2	12.5
Cryptantha virgata									x	10							x	1	12.5
Delphinium geyeri					0.1	5					0.1	10					0.1	2	25.0
Descurainia pinnata							0.1	10									0.1	1	12.5
Draba nemorosa	0.1	40	x	5	x	10									0.1	15	0.1	9	50.0
Erigeron flagellaris															0.1	5	0.1	1	12.5
Eriogonum alatum			0.1	10	0.2	15	0.1	5	0.2	20					0.2	15	0.2	6	62.5
Eriogonum effusum											1.0	80					1.0	10	12.5
Erysimum asperum					0.1	5							0.1	10	0.1	5	0.1	2	37.5
Euphorbia fendleri			0.1	5	0.1	5									0.1	10	0.1	2	37.5
Euphorbia robusta			0.1	5													0.1	1	12.5
Evolvulus nuttallianus	0.2	30	0.4	40	0.3	35	0.3	25	0.2	20	0.6	60	0.2	20	0.3	25	0.3	32	100.0
Gaillardia aristata					0.1	10			0.1	10			0.1	10			0.1	4	37.5
Gaura coccinea	0.3	30	0.6	55	0.2	25	0.5	50	0.4	50	0.3	40	0.5	50	0.3	30	0.4	41	100.0
Gilia inconspicua											0.1	10					0.1	1	12.5
Gutierrezia sarothrae			0.2	15					0.3	30	0.2	10					0.2	7	37.5
Haplopappus spinulosus	0.1	10					0.1	5			x	10			0.1	10	0.1	6	50.0
Helianthus pumilus	0.1	20	0.6	50	0.9	80	0.7	35	0.5	40	0.2	30	0.3	20	1.0	60	0.5	42	100.0
Hybanthus verticillatus	0.3	30															0.3	4	12.5
Lactuca scariola							0.1	5									0.1	1	12.5
Lappula redowski	0.1	10	x	5			0.1	5	x	10	x	10			x	10	0.1	7	75.0
Lesquerella montana							0.1	5									0.1	1	12.5
Liatris punctata			0.1	10	0.3	30	0.2	15	0.1	10	0.1	10	0.5	50	0.2	15	0.2	17	87.5
Linum lewisii			0.1	10	0.1	10	0.2	10	0.1	10							0.1	5	50.0
Lithospermum incisum	0.1	10	0.1	10													0.1	2	25.0
Lithospermum multiflorum					x	5	0.1	10			0.1	10			0.1	10	0.1	4	50.0
Lomatium orientale									x	30	0.1	10					0.1	5	25.0
Mertensia lanceolata							0.1	10					0.1	10	0.1	5	0.1	3	37.5
Mirabilis linearis			0.1	5	x	5	0.1	10	0.1	10							0.1	4	50.0
Musineon divaricatum	x	10	0.3	20	1.0	100	0.3	35					0.1	10			0.3	22	62.5
Oenothera brachycarpa									0.3	30							0.3	4	12.5
Orobanche fasciculata							x	5									x	1	12.5

TABLE I (Continued)

Analysis number	F1		F2		F4		F6		F8		F9		F7		F5		Ave. cover	Ave. frequency %	Constancy %
Date, 1953	7-6		7-6		7-14		7-17		7-23		7-23		7-21		7-17				
Number of m² sample areas	10		20		20		20		10		10		10		20				
Slope; direction, degrees	E 15		W 30		ESE 5-10		E 15		W 25		W 10-15		W 10-15		W 10-15				
Total number of species	23		36		40		43		41		40		41		49				
Ave. no. species per m²	8.3		10.4		11.5		13.0		12.3		11.3		15.5		13.2				
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F			
Orobanche uniflora													x	10			x	1	12.5
Oxytropis lambertii			0.1	5											0.1	10	0.1	2	25.0
Paronychia jamesii					0.1	10	0.1	10	0.3	30	0.1	10			0.1	5	0.1	8	62.5
Penstemon angustifolius			0.1	5	0.1	5			0.1	10	0.1	10	0.4	40	0.1	10	0.1	10	75.0
Petalostemum candidum									0.1	10	0.1	10					0.1	2	25.0
Petalostemum purpureum							0.1	5					0.1	10	0.5	50	0.2	8	37.5
Psoralea tenuiflora	0.2	20	0.8	75	0.7	70	0.5	45	0.9	80	0.6	60	0.4	40	0.3	30	0.6	50	100.0
Ratibida columnifera							0.2	15					0.2	10			0.2	3	25.0
Scutellaria brittonii					0.1	10	0.7	70					0.2	20	0.4	35	0.3	17	50.0
Senecio fendleri			x	5									0.2	20	0.2	25	0.2	6	37.5
Senecio spartioides									0.1	10							0.1	1	12.5
Senecio sp.					x	5	0.2	30									0.2	4	25.0
Sphaeralcea coccinea	0.5	50	0.1	5	0.3	35	0.5	50	0.3	30	0.4	40	0.3	30	0.3	30	0.3	30	100.0
Thelesperma megapotamicum			0.4	35	0.2	15	0.3	25	0.4	40	0.3	30	0.1	10	0.4	35	0.3	24	87.5
Tradescantia occidentalis							0.3	30	0.1	10	0.1	10	0.3	30	0.1	10	0.2	11	62.5
Tragia urticifolia									0.1	10							0.1	1	12.5
Tragopogon pratensis			0.1	5			0.1	5							0.1	5	0.1	2	37.5
Vicia americana									x	20							x	2	12.5
Viola nuttalliana	0.1	20	0.5	55	x	5											0.2	10	37.5
Neobesseya missouriensis					0.1	10					0.4	40	0.4	40	0.1	5	0.2	12	50.0
Opuntia polyacantha	0.1	10	0.2	15	0.3	20	0.4	35	0.6	60	0.7	60	0.5	50	0.1	10	0.4	32	100.0
Rhus trilobata															0.2	5	0.2	1	12.5
Rosa arkansana													0.4	30			0.4	4	12.5
Yucca glauca			0.1	5			0.1	5	0.3	30					0.1	10	0.1	6	50.0

only 8.3, ranging from 6 to 10, and the total number of species in the 10 quadrats was only 27. According to the Sörensen coefficient of similarity the vegetation of this stand resembled more closely that of stands F4, F2, F8, and F9 than the other three (Table III).

Stand F2 was located on the upper part of the same Morrison limestone ridge as F1, at the same elevation, but on the west-facing slope (Fig. 2). The slope of about 30° was steeper than in F1. The area comprised about 5 acres. The rockier, lower part of the slope was covered with a *Cercocarpus montanus* community marked by a sharp ecotone. The soil conditions (Table IV) were similar to those in F1 except that the sand content was less and the clay content greater at 6-18 inches (48-50 per cent), and the color was much paler, varying from gray brown at 4 inches to light gray or gray at 18 inches. The steep west slope was more exposed to the sun and wind and the runoff was greater, so conditions were more xeric than in F1. Rocks were scattered over the surface. The soil between 1 and 5 inches was fairly compact, below that it was looser. Stones and gravel were more numerous in the upper 8 inches than deeper. These more xeric conditions and less fertile soil were reflected in the more pronounced bunchgrass type of physiognomy as compared with stand F1. The clumps of *Stipa comata* were from 4 to 6 inches apart and the cover of *Bouteloua gracilis* in the lower layer was about a third less than in F1. The total number of species in 20 one-meter² quadrats was 36, the average per quadrat 10.4 (range 7-14). In contrast to F1, the distribution of species in frequency classes was normal (Table II). This, and the species number-area curve (beginning to flatten at 13 quadrats), and the distribution of species in the stand table indicate a high degree of homogeneity in the vegetation, except for an occasional clump of *Cercocarpus montanus* on rocky outcrops (Fig. 1). The greatest similarity was with stand F4, index of 76.0 per cent, the

FIG. 2. Stand F2 on Morrison limestone. *Gutierrezia sarothrae* and *Psoralea tenuiflora* are scattered among the grasses, chiefly *Stipa comata* and *Bouteloua curtipendula*. Shrubs are *Cercocarpus montanus*. July 6, 1953.

TABLE II. *Number of species in frequency classes I to V*

Stand	I	II	III	IV	V	Total
	0-20 %	21-40 %	41-60 %	61-80 %	81-100 %	
F1	11	7	1	1	3	23
F2	21	6	4	1	4	36
F4	24	6	3	2	5	40
F5	29	11	3	1	5	49
F6	21	10	6	3	3	43
F7	19	9	5	3	5	41
F8	23	10	3	1	4	41
F9	23	9	4	2	2	40

highest of all indices (Table III). High indices also occurred with F8 and F1; but very low with F7 (44.3 per cent).

Stand F4 was situated at an elevation of about 5,550 feet on an east to southeast slope of 10 to 15° of a Morrison limestone ridge rising above a small perched valley formed by a resistant outcrop of Dakota sandstone (Fig. 1) This was on the same ridge as the two preceding stands, but about 3/4 of a mile north. The area was about 4 to 5 acres. The stand formed a sharp ecotone on the east with a *Cercocarpus montanus-Pinus ponderosa* community on the outcrop of Dakota sandstone, and another ecotone on the west side where *Cercocarpus* formed a stand on the upper, rocky part of the limestone ridge. The soil closely resembled that of F1, especially in color which was dark gray brown at 4 inches and brown at 18 inches. There were fewer rocks on the surface, and more gravel and sand at 0-6 inches in F4 (Table IV). The stones and gravel were most numerous in the 0-6-inch layer, scattered throughout at 6-18 inches. Lime flecks appeared at 6 inches and increased gradually to 18 inches. The vegetation had a bunchgrass aspect (Fig. 1), due largely to *Stipa comata,* with uniform and relatively large cover. *Bouteloua curtipendula* had about half as much cover and was uniformly distributed. Except for a few scattered shrubs of *Cercocarpus montanus* on rocky spots, and a few *Rhus trilobata,* the stand presented a very uniform physiognomy. As shown in Figure 1, the spaces between the grass bunches were well-occupied, especially by such uniformly distributed species as *Sitanion hystrix, Bromus japonicus, Musineon divaricatum, Helianthus pumilus, Psoralea tenuiflora,* and *Artemisia frigida. Bouteloua gracilis,* however, varied considerably in cover and in distribution. The indices of similarity to the other stands, ranging from 53.0 to 76.0 per cent (Table III), show that there was more resemblance between this stand and the other seven than between any other stand and the rest. All except one of the indices were above the average of the 28 indices. The total number of species was 40, the average per quadrat 11.5 (range 8-17). The distribution of species in frequency classes was normal (Table II) and the species number-area curve reached a level at 15 quadrats.

TABLE III. *Indices of similarity, in percentage, based on cover estimates in Table I*

Stand	F1	F2	F4	F6	F5	F7	F8	F9
F1	.....	66.1	68.7	49.7	50.2	45.7	61.9	61.7
F2	.....	.....	76.0	64.3	54.6	44.3	71.9	58.6
F4	.....	.....	.....	62.6	61.0	53.0	71.9	62.1
F6	.....	.....	.....	.....	62.6	64.2	62.0	53.0
F5	.....	.....	.....	.....	.....	66.8	57.2	54.7
F7	.....	.....	.....	.....	.....	.....	52.4	53.0
F8	.....	.....	.....	.....	.....	.....	.....	69.4

Stand F6 was on the east-facing slope of a Morrison limestone ridge, on the same outcrop as F4, but separated from it by a small valley. The elevation was about 5,450 feet, the slope about 15°, and the area about 3 acres. The 20 quadrats were located about midway between the top and the bottom of the slope. Rocks were numerous, covering about 10 to 15 per cent of the surface. It was difficult to dig a profile pit, even to only 18 inches, because of the many rocks and pebbles which comprised 50 per cent or more of the soil volume. It was more rocky than the stands already described. The soil between the rocks had well-developed structure. It was hard at 3-10 inches, less so above and below this layer. As usual the surface inch was a loose, finely granulated mulch containing fragments of plants. The color was dark brown at 4 inches, pale brown at 18 inches; not as dark as in F1 and F4, but darker than F2. The texture (Table IV) was sandy clay at 0-12 inches and clay loam at 12-18 inches. The gravel and sand contents were moderately high throughout. The cover was excellent. The total number of species was 43, the average per quadrat 13 (range 9-17). Twelve species of grasses were present. The species number-area curve rose sharply in the first 8 quadrats, was fairly level to 16 quadrats, rose sharply at 17, and then levelled off again. The number of species in the higher frequency classes was greater than usual (Table II). This stand showed moderately high indices of similarity to stands F5 and F7, 62.6 and 64.2 per cent, respectively. These three stands formed a group of moderately high similarity to one another, and all three showed low similarity to F1. These three stands also showed greater similarity to an *Andropogon scoparius* stand in the vicinity than did any of the other stands. This stand was not as typical of the asso-

TABLE IV. *Soils data for the 8 stands in the Stipa comata-Bouteloua gracilis-B. curtipendula association*

Stand	Depth (inches)	pH	Effervescence*	Gravel %	Sand %	Silt %	Clay %	Texture class	Underlying rock
F1.....	0-6	8.0	VS	20.5	38.1	30.3	31.6	clay loam	Morrison limestone
	6-12	8.0	VS	10.5	28.1	33.0	38.9	clay loam	
	12-18	7.6	VS	9.6	22.4	37.0	40.6	clay loam	
F2.....	0-6	8.2	VS	18.8	33.1	33.1	33.8	clay loam	Morrison limestone
	6-12	8.2	VS	12.6	18.7	33.3	48.0	clay	
	12-18	8.0	VS	11.1	12.2	38.1	49.7	clay	
F4.....	0-6	8.2	VS	32.0	45.2	24.8	30.0	sandy clay loam	Morrison limestone
	6-12	8.2	VS	4.8	28.6	32.7	38.7	clay loam	
	12-18	8.2	VS	7.7	25.5	34.0	40.5	clay	
F6.....	0-6	8.0	W	13.6	57.4	19.4	23.2	sandy clay loam	Morrison limestone
	6-12	8.2	VS	5.4	51.0	23.8	25.2	sandy clay loam	
	12-18	8.2	VS	21.6	37.4	26.0	36.6	clay loam	
F8.....	0-6	7.4	W	35.1	24.0	54.0	22.0	silt loam	Dakota sandstone
	6-12	8.0	VS	86.5					
F9.....	0-6	8.2	VS	13.2	52.8	33.2	14.0	loam	Dakota sandstone
	6-12	8.2	VS	84.8	48.8	38.2	13.0	loam	
F7.....	0-6	7.0	VVW	15.0	26.0	22.0	52.0	clay	Dakota sandstone
	6-12	7.0	VVW	7.4	22.8	27.2	50.0	clay	
	12-18	7.0	VVW	37.8	26.8	25.2	48.0	clay	
F5.....	0-6	8.0	S	22.6	61.4	20.0	18.6	sandy loam	Morrison limestone
	6-12	8.2	VS	24.6	49.4	26.0	24.6	sandy clay	
	12-18	8.2	VS	22.9	27.4	38.0	34.6	clay loam	

*VS, very strong; S, strong; W, weak; VVW, very weak.

ciation, nor as homogeneous as most of the other stands.

Stand F5 (Fig. 3) was about ½-mile north of F6, near the top of the same Morrison limestone ridge, at an elevation of about 5,550 feet. The westward slope was about 10°, and the area about 2 acres. As shown in Fig. 3, rocks were scattered over the surface, and they were numerous to a depth of 12 inches, but sparse at 12-18 inches. The gravel and sand contents were high throughout, especially at 0-12 inches (Table IV). The soil texture was sandy loam at 0-6 inches, sandy clay at 6-12 inches, and clay loam at 12-18 inches. The clay content increased rapidly with depth. As usual, the reaction was moderately alkaline and the lime content, as shown by the effervescence with HCl and lime encrustations, was high. Lime flecks appeared at 5 inches, and increased rapidly with depth. Below 12 inches, the soil was more gray than brown. The color was uniformly dark brown to 5 inches, then gradually became paler, and at 18 inches was variegated gray brown to light gray. It was paler in color at the lower depths than in stands F1 and F4. The soil was also somewhat more rocky and contained more gravel and sand than those stands. The vegetation had a bunchgrass aspect (Fig. 3) and its density was greater than in any of the other stands. The total number of species was 49, the highest in any of the stands. The average number of species per quadrat was 13.2 (range 8-18). The species number-area curve was somewhat abnormal in that it reached a level at 10 quadrats with 38 species, rose again between 13 and 18 quadrats, and then reached a level at 48-49 species. The grasses with the greatest frequency and cover were in order, *Bouteloua gracilis, Aristida longiseta, B. curtipendula, Stipa comata, Bromus japonicus,* and *Andropogon gerardi* (Table I). Eleven species of grasses and one sedge were pres-

FIG. 3. Stand F5 on Morrison limestone. Clumps of *Andropogon scoparius, A. gerardi,* and *Aristida longiseta* are scattered among *Bouteloua gracilis, B. curtipendula,* and *Stipa comata. Helianthus pumilus* is frequent on the right. July 17, 1953.

ent. This stand was less homogeneous than many of the other stands because of the variability in the number of species per quadrat and in the cover of *Stipa comata, Bouteloua gracilis, B. curtipendula, Andropogon* spp., *Helianthus pumilus,* and *Artemisia frigida.* Stand F5 showed greatest similarity to stand F7 with an index of 66.8 per cent (Table III). The lowest index is with F1, 50.2 per cent.

Stand F8 (Fig. 4) was located about ½-mile southeast of Stand F1, on the west-facing slope of about 25° on a low Dakota Formation ridge. The elevation was about 5,360 feet and the area about 2 acres. Many large sandstone rocks occupied about 15 per cent of the surface and were also present in the soil to a depth of about 5 inches. Shale rocks which could be easily broken appeared at about 5 inches and increased rapidly in number so that below 8 inches small rocks were so numerous that it was practically impossible to secure a soil sample for laboratory analysis. The surface inch was loose and finely granular. The silt loam between the rocks at 0-6 inches was moderately hard, with well-developed structure. The gravel content was high, 35.1 per cent at 0-6 inches, 86.5 per cent at 6-12 inches (Table IV). The pH and lime content at 0-6 inches were somewhat less than in most of the stands. The color at 4 inches was dark gray brown, changing sharply to light gray brown at 12 inches. As compared to stand F4, the vegetation was more open. The regular distribution of *Stipa comata* and the occasional occurrence of the tall forb, *Eriogonum alatum,* gave the vegetation a bunchgrass appearance. Other conspicuous forbs were *Helianthus pumilus, Psoralea tenuiflora,* and *Yucca glauca.* The species with the highest frequency and greatest cover were in order, *Stipa comata, Bouteloua curtipendula, B. gracilis, Bromus japonicus,* and *Psoralea tenuiflora.* Because of the uniformity in cover and in dispersal of these species, the stand had a high degree of homogeneity. The total number of species in 10 quadrats was 41, the average 12.3 (range 9-16). The distribution of species according to the frequency classes was normal, as shown in Table II. The greatest similarity was with F2 and F4 (Table III) with an index of 71.9, and with F9 with an index of 69.4. The least similarity was with stands F7 and F5 with indices of 52.4 and 57.2, respectively.

Stand F9 (Fig. 5) was located on a west-facing slope of 10-15° on the same low Dakota ridge. The elevation was slightly lower than that of F8, about 5,340 feet. It comprised 2 to 3 acres. Very few rocks occurred on the surface, in contrast to F8. Small dark gray shale rocks which were readily broken appeared at 5 inches and increased markedly with depth so that below 8 inches very little soil was found. The gravel content increased from 13.2 per cent at 0-6 inches to 84.8 per cent at 6-12 inches. Below 12 inches it was too rocky to secure a sample (Table IV). At 0-12 inches, the sand content was high, the clay content low. Bare ground comprised about ¼ of the surface. The color of the soil was not as dark as in most of the stands, ranging from gray brown at 4 inches to light brown at 12 inches. As in stand F8, the vegetation was the open bunchgrass type, composed chiefly of *Stipa comata,* with a lower layer of mostly *Bouteloua gracilis.* This stand was not as homogeneous as most of the other stands. Although *Stipa* showed much uniformity, *B. gracilis* was more spotty, and *B. curtipendula* and *Bromus japonicus* were less uniform and less abundant than in the other stands (Table I). The most numerous forbs were *Eriogonum effusum, Evolvulus nuttallianus,* and *Psorolea tenuiflora.*

FIG. 4. Stand F8 on low Dakota sandstone ridge. Tall *Eriogonum alatum, Psoralea tenuiflora,* and *Helianthus pumilus* are the most conspicuous forbs among the grasses; *Stipa comata, Bouteloua curtipendula,* and *B. gracilis. Cercocarpus montanus* is on the ridge top. July 23, 1953.

FIG. 5. Stand F9 on lower part of the same ridge, Dakota sandstone, as shown in Figure 4. Chief grasses are *Stipa comata and Bouteloua gracilis. Psoralea tenuiflora, Eriogonum effusum,* and *Artemisia frigida* are scattered. July 23, 1953.

The total number of species in 10 quadrats was 40, the average per quadrat 11.3 (range 9-17). The distribution of species in frequency classes was somewhat abnormal in that class IV was the same as in class V. The index of similarity to the other seven stands is below average; the highest index, 69.4, is with F8, the lowest with F6 and F7, 53.0 per cent.

Stand F7 was situated at an elevation of about 5,400 feet on a low Dakota Formation ridge about 0.2 mile north of F6 (Fig. 6). The 10-15° slope faced westward. Rocks of Dakota sandstone were numerous on the surface and a few were scattered in the upper 6 inches of soil. Below 6 inches, particles of shale appeared. The surface inch was very loose. Between 1 and 8 inches, the clay soil was very hard with well-developed block structure, the aggregates having flat surfaces and sharp edges, breaking with difficulty. The clay content was higher than in any of the other stands, ranging from 52.0 per cent at 0-6 inches to 48 per cent at 12-18 inches (Table IV). The gravel content was low at 0-12 inches, fairly high at 12-18 inches. The soil reaction was lowest of all stands, pH 7.0 from the surface to 18 inches. The effervescence was very weak. The color at 4 inches was dark gray brown, at 12 inches light gray brown. The total number of species in 10 quadrats was 41, the average 15.5 (range 13-19) the highest in the eight stands. There were 15 species of grasses, compared to 7 to 12 in the other stands. The number of species in frequency class I was slightly lower than usual and there were 5 species in class V (Table II). Because of the lesser abundance of *Stipa* and the fairly dense growth of other grasses, the vegetation did not have as pronounced a bunchgrass physiognomy as in many of the other stands. The stand showed considerable homogeneity, in spite of the smaller cover than usual of *Stipa*. This was due to the uniform distribution of *Koeleria cristata, Bouteloua curtipendula, Bromus japonicus, Aristida longiseta, Stipa comata,* and the higher frequency than usual of a number of forbs (Table I). As shown in Table III, the similarity of stand F7 to the other stands ranges from the very low index of 45.7 with F1, 44.3 with F2, to the fairly high index of 66.8 with F5. Stand F7 formed a group with F5 and F6 on the basis of high indices of similarity.

FIG. 6. Stand F7 on a low Dakota sandstone ridge, Chief grasses are *Bouteloua gracilis, B. curtipendula, Koeleria cristata, Bromus japonicus,* and *Stipa comata. Liatris punctata, Artemisia ludoviciana,* and *A. frigida* are scattered. July 21, 1953.

PHYTOSOCIOLOGICAL DATA AND ANALYSIS

Analysis of Table I reveals that there are 3 dominants and 12 constants in these 8 stands. Constants are species which occur in 80 per cent or more of the stands. The dominants are *Stipa comata, Bouteloua curtipendula,* and *B. gracilis.* The relative importance of these three is shown by the figures of average cover: 2.7, 1.7, and 1.6 respectively; the average frequency: 99, 92, and 73 per cent respectively; and the constancy, 100 per cent for each. The constants with the highest cover and medium frequency were from high to low: *Bromus japonicus, Aristida longiseta, Psoralea tenuiflora, Helianthus pumilus, Sitanion hystrix,* and *Gaura coccinea.* Constants with low cover and medium frequency were in order from low to high: *Evolvolus nuttallianus, Opuntia polyacantha, Sphaeralcea coccinea, Thelesperma megapotamicum,* and *Liatris punctata. Artemisia frigida* was fair in cover, high in frequency.

The species in each of the stands were classified according to their average frequencies into 5 classes, as shown in Table II.

Six of these stands show normal ratios, namely $I > II > III \gtreqless IV < V$, but in stands F6 and F9 the ratio is $IV = V$, indicating somewhat less homogeneity than where V is greater than IV. In stand F6, only three grasses occur in class V, whereas usually more grasses usually occur in this class. In stand F6 also a higher number of species than usual occurs in class IV, of which two are the rhizome-bearing *Artemisia ludoviciana* and *Scutellaria brittonii.* Stand F9 had the unusually low number of two species in class V, *Stipa comata* and *Bouteloua gracilis.*

The average number of species per quadrat varied from 8.3 in stand F1 to 15.5 in F7. The total number of species in all of the quadrats per stand varied from 23 in stand F1 to 49 in F5. The latter stand had more forbs, especially in frequency class I, than stand F1 or the other stands.

The species number-area curves showed a general tendency to flatten at 8 quadrats. This was more pronounced in stands F2 and F6 than in F4

and F5. The last one showed a secondary rise between 12 and 16 quadrats. One may conclude that 20 meter-square quadrats are more than sufficient for sampling this kind of vegetation, but that 10 are near the lower limit, if not below, in some stands; so 20 are recommended for future use.

In order to determine differences and similarities between the stands Sörensen's index of similarity (Sörensen 1948, Nordhagen 1943) was calculated for each pair of the 8 stands, giving a total of 28 indices (Table III). The following formula was used: $K_s = \frac{2c.100}{a+b}$, in which K_s is the index between two stands, *a* represents the sum of the averages of cover of all species in stand A, *b* the similar figure for stand B, and *c* the part of the cover common to the species found in both stands. For example, in comparing stands F1 and F2, *c* is obtained by adding 0.5 for *Aristida,* 1.9 for *Bouteloua curtipendula* in F1 because the same degree of cover is found also in F2, 0.8 for *B. gracilis* in F2, etc. The total is then multiplied by 2 as required in the formula. If the similarity is perfect the index would be 100 per cent; if there is no similarity the index would be 0. The index of similarity was also calculated between every pair of stands using species presence instead of cover. In this calculation, *c* in the formula represented the number of species common to the two stands being compared, *a* the number of species in one stand, *b* the number of species in the other stand. These indices ranged from 44.4 per cent between stands F1 and F5 to 69.0 between F5 and F7, with an average of all pairs of 58.8 per cent, compared to 60.0 per cent when cover figures were used.

The indices of similarity based on cover range from a low of 44.3 per cent between F2 and F7 to 76.0 between F2 and F4. The average of the 28 indices is 60.0. Six of the stands can be grouped into 4 groups on the basis of their high similarity to F4 and to one another. These groups are 4-1-2 and 4-2-8 with high similarity to one another, and 4-5 and 4-8-9 with less similarity. Stand 6 also shows moderate similarity to the second group. The stands in the second group, 2-4-8, show especially high similarity to one another. According to this analysis, stand F4 may be considered one of the best examples of the stands studied as representative of the *Stipa comata-Bouteloua gracilis-B curtipendula* community because of the high indices of similarity to most of the other stands, and also for other reasons such as the kinds of species present in it, the normal distribution of species in the species number-area curve, and the total and average number of species per quadrat. It appears that Stand F4 can be used as a norm or standard for assessing the condition of other stands in this kind of community and for comparing degrees of similarity. If the difference of another stand with this stand is large, it would probably have to be classified in another kind of community. Stand F4 is apparently the most suitable for detailed studies of the vegetation in relation to soil and climatic conditions, effects of grazing, phenological studies, and others. If a pair, or more, of stands is needed for replication of treatments, it seems that the most suitable would be those that show a high degree of similarity to F4, such as F2 and F8. This procedure may be applicable to grassland types generally and lead to greater control of experimental error.

The stands F5, F6, and F7 show moderately high similarity to one another and low similarity to F1. This group of three is characterized by lesser abundance of *Stipa comata* and by greater abundance of *Andropogon gerardi, Aristida longiseta, Koeleria cristata, Artemisia frigida, A. ludoviciana,* and *Scutellaria brittonii.* It shows greater similarity to a typical *Andropogon scoparius* stand, which occurred in the vicinity, than do the other groups. The index of similarity of the stands in the 5-6-7 group to the *Andropogon scoparius* stand ranges from 45.1 to 48.1 per cent, while in the stands in the 2-4-8 group the index of similarity ranged from 36.1 to 38.9. Stands F1 and F9 show even less similarity to the *Andropogon* stand with indices of 22.5 and 25.8 respectively.

Discussion

The variations in topographic and soil conditions, as described under the stands, while often considerable in texture, degree and direction of slope, and rockiness, were within the ecological amplitude of the chief species (Table IV). Stands on west-facing slopes, as F2 and F8, had a more pronounced bunchgrass physiognomy than the other stands, but on the whole, steepness and direction of slope had apparently little influence on species composition. The soil reaction was least alkaline and lowest in lime content in F7 in which the number of species was highest and in which *Koeleria cristata* and *Carex heliophila* had the greatest cover. No outstanding relationship was found between species composition of the stands and the contents of gravel and sand in the soil profiles, and little relationship appeared with respect to clay content. The lowest clay content was found in F9, the only stand in which *Eriogonum effusum* and *Gilia inconspicua* occurred. The vegetation on the Dakota Formation usually appeared more weedy than that on the Morrison

limestone, and the analyses showed greater abundance of such species as *Bromus tectorum, Ambrosia psilostachya, Tragia urticifolia,* and the cacti. Several forbs, including *Gilia inconspicua, Oenothera brachycarpa, Erigonum effusum, Petalostemum candidum, Rosa arkansana,* and *Senecio spartioides* occurred only on the Dakota in these analyses. *Draba nemorosa* was found only in stands on the Niobrara limestone.

Stands resemble one another because of the presence of many of the same species in each, and because of the common abundance of these species as indicated by herbage cover. If the total number of species common to two stands is high, and if the abundance of these common species is also similar, then the degree of similarity, or homology, of the two stands will be high. The highest degree of similarity should be found in the data of two different sets of quadrats taken from the same stand on the same day. Even such data would not give an index of 100 per cent because of the variation in micro-conditions sampled by the quadrats within one stand which would cause differences in the dispersal of species, and also because of differences in the distribution and abundance of species due to chance or aggregation. Indices of 65 per cent or more (based on cover data) indicate a high degree of homology. Of the 28 indices of similarity between the 8 stands 7 are 65 per cent or higher and 9 more are between the average index of 60 per cent and 64. Two are low, 44.4 per cent for F2 and F7 and 45.3 per cent for F1 and F7. The minimum coefficient of similarity that forms the limit for classifying a stand in a certain kind of community cannot be determined by data available in this study. It is doubtful also if it would be valid to use the coefficient of similarity as the sole criterion in the classification of stands into communities. It appears, however, that indices as low as 44.3 and 45.3 are near or at the border line, even though the resemblances in physiognomy and dominant species are strong. This view is supported by finding similar indices (42.2 and 48.1) between F5 and F7 with a distinctive *Andropogon scoparius* stand in the same region.

On the basis of the 8 stands analyzed in this paper and the 10 stands studied by Hanson and Dahl (ms.), the *Stipa comata-Bouteloua gracilis-B. curtipendula* association is characterized as follows:

Dominants: *Stipa comata, Bouteloua gracilis, B. curtipendula. Stipa* is the most important.

Constants: *Bromus japonicus, Aristida longiseta, Sitanion hystrix, Evolvulus nuttallianus, Gaura coccinea, Helianthus pumilus, Liatris punctata, Psoralea tenuiflora, Sphaeralcea coccinea, Thelesperma megapotamicum, Artemisia frigida,* and *Opuntia polyacantha.*

The physiognomy of this association is the bunchgrass type, with medium to small bunches. Two prominent layers occur, the upper, 1 to 2 feet tall, composed chiefly of *Stipa comata* and tall forbs; the lower, about 3 to 5 inches high, composed chiefly of the other two dominants. The herbage cover (ungrazed) is variable, from about 25 to 85 per cent. The number of species is moderately high, averaging 33 in 18 stands and ranging from 22 to 49 per stand, and from 8.3 to 15.5 per quadrat. The largest number of species are perennial herbs, the annual herbs and shrubs or half-shrubs are very few. The index of similarity between pairs of stands varies from 44.3 to 76.0 per cent. The relationship with the *Andropogon scoparius* association is close. The *Stipa-Bouteloua* association occurs usually on moderate to steep upper slopes, most often in calcareous soil, moderately alkaline in reaction. Rocks and gravel are common and often numerous on the surface and in the profile. The soil is shallow, texture is not very compact, consisting most often of sandy loam in the upper 6 inches. The soil is fairly well-developed, usually dark brown at 0-12 inches, brown to gray brown at 12-18 inches. Water penetrates readily and is adequate in most years for a moderately long growing season. Erosion is slight to none and usually there is no deposition. The range in soil conditions suitable for the development and maintenance of this community is wide. This is significant in connection with the idea expressed by Gardner and Retzer (1949) that the range of characteristics permissable in a single soil series in nonarable range land should be somewhat broader than for a soil series in arable land. This association is resistant to invasion by *Bromus tectorum.* It furnishes excellent grazing for cattle and sheep. It may be considered as one of the chief climax types in this region.

Summary

The purpose of this study is to characterize the *Stipa comata-Bouteloua gracilis-B. curtipendula* community on the basis of descriptions of stands occurring within a limited region. The chief analytical characteristics used are species composition, herbage cover, and the dispersal or frequency of individuals of each species. Attention was also given to stratification, periodicity, vitality, lifeform, and height. The synthetic characteristics, constancy and presence, were also used. The data are summarized in an association table and were analyzed by means of the frequency classification, species number-area curves, and Sören-

sen's index of similarity. Data on soil characteristics, including texture, approximate lime content, pH, and color were secured.

Eight stands were selected for analysis on the basis of similarity in physiognomy and the presence of the same dominant and other leading species. These stands are classified in the *Stipa comata-Bouteloua gracilis-B. curtipendula* association because of the dominance of at least two of these species in each stand and because of the high degree of floristic homology prevailing in them. The most important species, in addition to the dominants, are the constants *Bromus japonicus, Aristida longiseta, Sitanion hystrix, Evolulus nuttallianus, Gaura coccinea, Artemisia frigida, Helianthus pumilus, Liatris punctata, Psoralea tenuiflora, Sphaeralcea coccinea, Thelesperma megapotamicum,* and *Opuntia polyacantha.*

The total number of species in 120 one-meter^2 quadrats in 8 stands was 89. The number of species per stand ranged from 23 to 49 and the average was 39.1. The average number of species per quadrat varied from 8.3 to 15.5.. On the basis of resemblances in indices of similarity, the 8 stands could be classified into groups. One group, F2-F4-F8, was the most homologous. Each stand is an entity with its own specific geographic location and characteristics. Because of the homology of the stands to one another they can be classified into one kind of abstract community.

The *Stipa comata-Bouteloua gracilis-B. curtipendula* association is tentatively characterized. Stands of this association occur over a fairly wide range or topographic and soil conditions in the mountain-front zone of northern Colorado. Its geographic range is not known. It is rather closely related to the *Andropogon scoparius* association in this region.

Analysis of the data indicates that one of the stands, F4, can be chosen as the most representative of those analyzed, and therefore most suitable for detailed study. When more stands are needed for replication, those with the highest index of similarity to this one appear most suitable. Such a typical stand may also be used as a criterion by which to determine the condition and stage of succession of other stands of this type.

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THE OCCURRENCE OF FIGHTING BEHAVIOR IN THE GRAIN BEETLE *TENEBRIO MOLITOR* WITH THE POSSIBLE FORMATION OF A DOMINANCE HIERARCHY[1]

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INTRODUCTION

When two animals meet, there are two general types of behavior that might be exhibited. One of these is equivalent behavior of tolerance or indifference, in which neither challenge nor submission is displayed. The other is nonequivalent behavior of active dominance and subordination. The manifestation of any of these phenomena varies from group to group.

Observations of the behavior of the grain beetle *Tenebrio molitor* suggest that there is a strong degree of domination exerted by some of the individuals over others. Evidences of this are found in laboratory cultures of the grain beetle in the frequent appearances of injuries to the living animals (larvae, pupae, and adults).

MATERIALS AND METHODS

The animals used for these experiments were kept in separate petri dishes (9 cm. in diameter) with filter paper in the bottom of each dish. Water was added to the paper daily in sufficient quantity to moisten, but not to soak the filter paper. When the animals were not being tested, they were kept in the dark.

During the experiments, the animals being tested were introduced into a clean petri dish with dry filter paper, rather than the moist paper like that in their own dishes. This was found necessary because the beetles spent most of their time chewing on the paper when moist paper was available, showing little or no reaction to each other. Each animal was given a catalog number, and this was written on the top of the dish. It proved unnecessary to mark the animals because they were tested only two at a time, and there is sufficient individual variation in this species for the observer to distinguish them. The variations include slight color differences (from reddish fuscous to black), differences in the length of the elytra of a given beetle, differences in the over-all lengths of the animals, differences in lengths of the elytra with respect to the abdomen, and various imperfections in the anatomy of the beetles, either from imperfect eclosion, or from the effects of cannibalism on the parts of other beetles.

The two animals to be tested at a given time were removed from their respective dishes in as close succession as possible to eliminate the possibility of any behavior due to territorialism, etc. If the beetle being transferred accidentally fell over onto its back, it was removed and not tested until an hour later. This eliminated any possible effects of the strong righting behavior (characteristic of beetles when they lose their balance) upon the other beetle with which the subject beetle was being tested. After the two beetles had been introduced into the test dish, it was covered, and the activities of the beetles were recorded. The animals were observed for as long a period as it took for them to exhibit a definite interrelationship of dominance or subordination. If no such demonstration was given after 90 minutes, the beetles were returned to their respective dishes and tested at a later time. This was seldom necessary.

RESULTS AND OBSERVATIONS

In *Tenebrio,* equivalent behavior is demonstrated in the following ways: a. mutual antennation; b. mutual palpation (each stroking the palpi of the other with his own); c. mutual investigation with antennae and palpi of each other's anatomy; d. lack of akinesis (akinesis is lowering of head, remaining motionless, allowing encountering animal to walk over, to bite it, etc.); and e. resisting attacks with counter-attacks.

Non-equivalent behavior is much more common with *Tenebrio* and has numerous forms of exhibition. This category is divided into dominant and subordinate sorts of behavior. The dominant may exhibit the following types of behavior: a. walk over subordinate, as if it were an inanimate object; b. mount (regardless of sex of subordinate), with or without exserting the aedeagus, in copulating orientation or the reverse; c. palpate or antennate (or both) the subordinate roughly; d. nudge the subordinate, pushing it either to the side or into the air; e. "butt" the subordinate, frequently knocking it some distance (this may be accomplished either by rushing the subordinate from a distance and striking with head directed forward, or by coming into contact

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with the subordinate beetle first, then lowering the head, digging under the subordinate beetle slightly with it, then suddenly elevating the head, thus throwing the subordinate into the air); f. knock the subordinate over, either by catching it off balance or by overturning it from a stable position; g. bite or nibble at the antennae, palpi, legs, or elytra of the subordinate; h. kick the subordinate; or, i. threaten the subordinate (this may be accomplished by rushing at the subordinate, then stopping suddenly, which usually causes the subordinate to avoid, or by standing face to face with the subordinate, conspicuously moving the mouth parts which also may evoke an avoiding reaction on the part of the subordinate).

Manifestations of subordination are fewer in number, but just as diagnostic in character as are the signs of dominance. The following reactions characterize the subordinates: a. general avoidance of the dominant, either by turning aside or reversing orientation and runing away; b. akinesis (see above); c. gentle antennation or palpation (or both) of the dominant.

The explanation of dominance or subordination is not always apparent, but there are some signs that are obvious. Size is often a determining factor. Almost without exception, within unisexual groups, when neither of the two animals being tested had any injury, the larger was the dominant. In mixed groups, the male was almost invariably dominant over the female, except when the female outsized the male by a wide margin. If a given beetle has recently emerged as an adult, it is extremely vulnerable, being soft and easy prey. These animals were always quiet and subordinate in their relationships with the older, more sclerotized (though not always larger) beetles. If a beetle had been injured, it would ordinarily assume a subordinate attitude in its contacts with other beetles. Lastly, as a beetle ages, it usually loses its dominant status gradually, just as the young beetles gain dominance as they grow older. In Table I, the constancy of the relatively subordinate positions of the beetles number DS2 and DS3 is noteworthy. The positions here may be attributed both to injury and to size. DS2 had an injured left antenna, and DS3 had one antenna completely missing. Both were smaller than DS1 and DS4. Since DS2 and DS3 were approximately the same size, the differences in their antennae may have been the cause of their positions with respect to each other.

The original plan was to have three types of experiments: a. all males; b. all females; and c. males and females mixed. But it was found that in contacts in the mixed groups, the female almost invariably adopted a subordinate attitude, which is part of the normal mating behavior. For this reason, it was found more feasible to study the reactions of each sex separately. In the first set of experiments, only males were used. In contrast to the constancy of the positions of DS2 and DS3, a marked shift in the relative positions of DS1 and DS4 was found. These beetles were of the same size, but DS4 was missing its right mesotarsus. This injury was of apparently little consequence, for DS4 attained dominance over another of its own size (DS1) which had no apparent injury.

TABLE I. *Dominance-Subordination Relationships Among Four Males on Successive Days*

Date (1951)	Beetle Number	Rank	Beetles Subordinated			
June 21	DS1	1	3	2	4	..
	DS4	2	3	2	..	..
	DS2	3	3	..	..	..
	DS3	4	..	..	..	..
June 22	DS1	1	3	2	4	..
	DS4	2	3	2	..	..
	DS2	3	3	..	..	..
	DS3	4	..	..	..	..
June 23	DS1	1	3	2	4	..
	DS4	2	3	2	..	..
	DS2	3	3	..	..	..
	DS3	4	..	..	..	..
June 24	DS1	2	3	2	..	..
	DS4	1	3	2	..	1
	DS2	3	3	..	..	..
	DS3	4	..	..	..	..
June 25	DS1	2	3	2	..	..
	DS4	1	3	2	..	1
	DS2	3	3	..	..	..
	DS3	4	..	..	..	..
June 26*	DS1	2	..	2	..	..
	DS4	1	..	2	..	1
	DS2	3	..	..	..	..
June 27†	DS1	1	..	..	4	..
	DS4	2	..	..	..	..

*DS3 died.
†DS2 died.

In the second group of tests, ten males were used, each beetle meeting each of the others three times. (DS7 and DS10 died after the first series of this group.) The results of this series are shown in Table II. It is apparent from a comparison of the three series in this table that there is a tendency toward gradual stabilization of dominance-subordination relationships among animals which encounter each other more than once. It may also be noted in Table II that there is a tendency toward "ties" in respective dominance ratings. In the first series, there was only one animal (DS13) which did not tie with another.

TABLE II. *Three Series of Dominance-Subordination Relationships Among Ten Males (DS Series)*

Beetle Number	Rank	Beetles Subordinated									
		Series 1									
13	1	5	6	8	9	10	7	14	11	..	..
12	2.5	5	6	8	9	10	7	..	..	..	13
11	2.5	5	6	..	9	10	7	14	..	12	..
14	7	..	6	..	..	10	..	..	..	12	..
7	7	..	6	..	..	10	..	14	..	..	..
10	7	5	6	..	9	..	..	..	..	..	..
9	4.5	5	6	8	..	10	7	..	..	..	..
8	4.5	5	..	..	..	10	7	14	11	..	..
6	9.5	5	..	8	..	..	..	..	..	..	..
5	9.5	..	..	..	..	..	7	14	..	..	..
		*Series 2**									
13	1	5	..	8	9	..	..	14	11	12	..
12	3	5	6	8	9	..	..	14	..	..	..
11	3	5	6	8	9	..	..	..	..	12	..
14	3	5	6	8	9	..	..	..	11	..	..
9	5	5	6	8	..	..	..	..	..	..	..
8	6.5	5	6	..	..	..	..	..	..	..	..
6	6.5	5	..	..	..	..	..	..	..	..	13
5	8	..	..	..	..	..	..	..	..	..	..
		*Series 3**									
13	2	5	6	8	9	..	..	..	11	12	..
12	2	5	6	8	9	..	..	14	11	..	..
11	4	5	6	8	9	..	..	..	..	..	..
14	2	5	6	8	9	..	..	..	11	..	13
9	5	5	6	8	..	..	..	..	..	..	..
8	6	5	6	..	..	..	..	..	..	..	..
6	7	5	..	..	..	..	..	..	..	..	..
5	8	..	..	..	..	..	..	..	..	..	..

*DS7 and DS10 dead.

In the second series, there were three animals with no ties, and in the third series, there were five without ties. In an analysis of dominance-subordination relationships among animals, the existence of such ties as are found here is often characteristic of groups with a less rigid type of social organization (Allee 1938). The interactions among the beetles in group DS5-14 are shown diagrammatically in Figure 1.

The third group of experiments involved a group of six females. The results of these experiments and observations are shown in Table III. In general, the sorts of dominance-subordination relationships are the same as with the groups of males. There is a conspicuous number of ties within each series. There are also several notable "triangles", as in the case of DS16, DS17 and DS18. The existence of such triangles is another characteristic of a less rigid type of social organization. In the triangle mentioned above, the organization in Series Two of this group was as follows: DS16 → DS17 → DS18 →DS16. Retesting of these three gave the following results: DS16 → DS17 → DS18, and DS16 → DS18. (The arrow is directed away from the dominant toward the subordinate.) The lack of significance of this retest is shown by the fact that DS16 ended up with the second lowest dominance frequency, despite the temporary successes en-

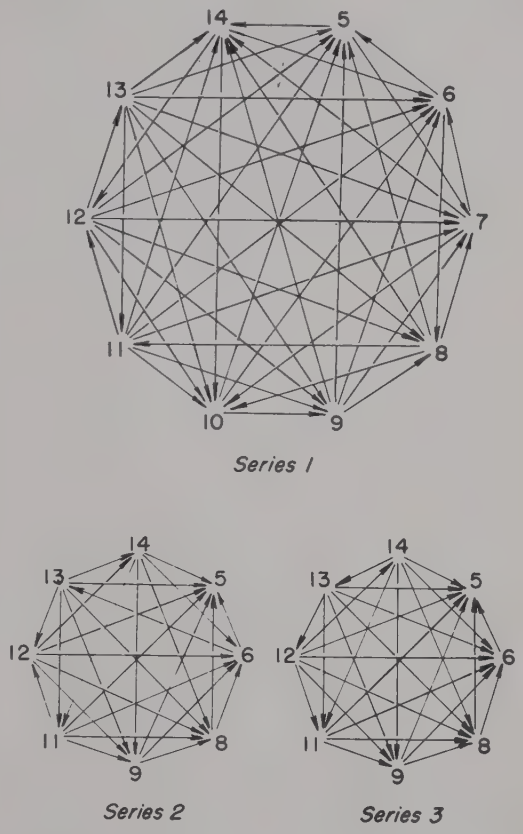

FIG. 1. Dominance-subordination relationships in male group *DS 5-14.*

TABLE III. *Two Series of Dominance-Subordination Relationships Among Six Females (DS Series)*

Beetle Number	Rank	Beetles Subordinated					
		Series 1					
15	2	20	16	..	18	17	..
17	2	20	16	19	18	..	..
18	4	20	16	..	..	..	..
19	2	20	16	..	18	..	15
16	5	20	..	..	..	..	..
20	6	..	..	..	..	..	..
		Series 2					
15	1	20	16	19	18	17	..
17	3	20	..	19	18	..	..
18	3	20	16	19	..	..	..
19	5	20	..	..	..	..	..
16	3	20	..	19	..	17	..
20	6	..	..	..	..	..	..

countered in this retest series. Retesting other triangles gave comparable results. This seems to emphasize the fact that among these animals, with their almost total lack of social behavior, there is not a strict linear dominance, but rather a relative separation of individuals into categories that may be characterized as "usually dominant," "usually subordinate," and "sometimes dominant". Another complication arises in the attempt to solve these triangles, in that there is a constant shifting in the dominance status of each animal, which may be attributed to injury, old age, maturing, threatening, etc. That any of these factors may also be operating during the solution of any of these triangles is obvious.

Discussion

It may be seen from the foregoing experiments and observations that relationships of dominance and subordination are not restricted to social animals (animals normally living in more or less organized aggregations), though it is among these where this phenomenon attains its fullest expression. Thus, there is the distinction between "peck right", as shown in flocks of hens, which have a strict linear dominance (Allee 1938; Collias 1944) and "peck dominance" which is more characteristic of a looser social organization. The latter type of organization is characterized by frequent triangles, shifts in social status, etc. This sort of organization may be found in canaries and parakeets (Allee 1938). Until further data on the invertebrates are available, it is perhaps unwise to propose an analogy between the behavior of any invertebrate and any vertebrate group. Regardless of its degree of development, the attribute of dominance may be employed in various ways by different animals. One of the most common of these is the establishment and maintenance of territories, as shown in birds (Howard 1920; Nice 1933), in lizards (Evans 1936), etc., among the vertebrates, and among the invertebrates, territorialism has been demonstrated in fiddler crabs (Crane 1941) and wasps (Pardi 1948). From the observations made on *Tenebrio,* however, no display of territorialism was given. It has been shown that there is not a strict dominance-subordination arrangement. The effect that the dominant and subordinate actions of the individuals has upon the population is that the dominants eventually prove to be the survivors. They are the individuals that are left after successive injuring encounters have finally killed the subordinates. And they are the ones which will be the reproducing individuals, thus showing a tendency to prevent reproduction by the weaker individuals.

There are several conflicting views concerning the significance of the phenomenon of dominance and subordination. It is the view of Schjelderup-Ebbe, based on observations on many species of birds, that "despotism is the basic idea of the world, indissolubly bound up with all life and existence. On it rests the meaning of the struggle for existence" (quoted in Allee 1938, p. 161). On the other hand, Allee adopts the view that "competition, by establishing degrees of dominance and subordination, whether in the ecological or human sense, may furnish a basis for more effective community cooperation. Such organized communities may then compete with each other and the less fit cooperating systems may be weeded out to the general advantage of the survivors at least" (Allee 1940, p. 160).

The two views are not mutually exclusive, though they might appear to be so at first glance. On the one hand, the activities of *Tenebrio* seem to fit into the "despotism" scheme of Schjelderup-Ebbe in that there never is built up a rigid scheme by which the animals can cooperate against other groups as a unit. But on the other hand, there is an advantage not only to the survivors (which is in accord with Allee's view), but also to the species population, in that only the strongest survive to reproduce.

Summary

1. A group of four males was tested on seven consecutive days for dominance and subordination. The dominant status of each individual was found to be commensurate with his size and degree of injury. The two larger beetles were consistently dominant over the two smaller beetles. Loss of a mesothoracic leg by one of the larger beetles seemed to have little effect on its dominant status, whereas loss of an antenna by one of the smaller individuals was the only apparent morphological difference which might have contributed to its consistently subordinate status, relative to the other beetle.

2. In a group of ten males, each met each of the others three times in trials for dominance and subordination. A tendency toward stabilization of relative dominance standings was found on subsequent encounters. Ties and triangles (A dominant over B, B over C, and C over A) were frequent. Retests of the triangles were inconclusive.

3. In a group of six females, each meeting each of the others twice, the results were similar to those found in the male group. Again, ties and triangles were characteristic.

4. Preliminary tests showed that in mixed groups, the female assumed the subordinate role

except when considerably larger than the male.

5. No linear order of dominance was established (as is characteristic of non-social animals). The individuals may best be characterized as "usually dominant", "usually subordinate", or "sometimes dominant".

6. Factors contributing to dominance are sex, size, degree of injury, and age as an adult (time from emergence from the pupal case).

7. A possible adaptive significance of such relationships of dominance and subordination is discussed briefly.

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OBSERVATIONS OF STEM ELONGATION IN CERTAIN TREES IN THE WESTERN ADIRONDACKS[1]

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Introduction

Although stem elongation of trees has been studied extensively, much remains to be learned regarding the factors which influence its periodicity during the growing season, and the relative amount of growth put on during successive growing seasons. Reviews of the extensive literature concerning height growth and its relation to air temperature, solar radiation, and other site factors have been prepared by Burger (1926), Hertz (1929), Baldwin (1931), Adams (1935), and Reed (1939), consequently specific reference is made here only to a few studies closely allied to the subject of this paper.

In a general statement, Sachs (1882) reported that growth of plants begins only after a certain lower temperature is passed, and that it increases its rate at higher temperatures until at a certain temperature point (the optimum) a maximum rapidity of growth is reached, and if the temperature increases still further, the growth rate decreases. He pointed out also that response to external conditions may be greatly affected by the phase of "the great curve of growth."

In this country, Illick (1919) was apparently the first to study seasonal height growth. He observed that species differed considerably in their progress of growth. Some continue without a break, others grow by "leaps and bounds," alternating with rest periods. Baldwin (1931), Tryon and Finn (1937), Keinholz (1941), and Cook (1941) observed that the seasonal course of height growth is very similar for the same species year after year. Burger (1926) reported that variations in temperature, although causing peaks and depressions, do not change the general shape of the growth curve.

Hiley and Cuncliffe (1922, 1923) studied the height growth of several species of trees growing in England. They found that the rate of elongation increased and decreased as the air temperature increased and decreased. They concluded that air temperature is much more important than all other factors put together in determining the variations in growth rate during the growing season. There was no direct correlation between actual increments of terminal elongation and actual temperature because the increment curve rose to pronounced maximum and decreased, while the temperature curve progressed increasingly higher throughout the period of most rapid growth. They concluded that a fall in the increment corresponding to a given fall in the air temperature is not a fixed amount, but is proportional to the rate of increment at the time.

An application of the great curve of growth concept to tree growth was made by Illick (1919). He stated that the seasonal growth of a tree begins slowly. After a variable time the growth rate increases rapidly, and reaches a maximum, which is

[1] Data for this paper were taken from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of the University of Michigan.

maintained for a short time. Then it decreases gradually to a minimum and finally ceases completely. Hiley and Cuncliffe (1922) and Reed (1939) prepared seasonal trend curves of terminal elongation for each species of tree studied. These curves were of the form described by Illick. Reimer (1949) also found that terminal elongation of five deciduous species followed the "grand period" type of curve.

Study Area

The Ranger School Forest of the State University of New York, College of Forestry is located on the western edge of the Adirondack Mountains in the Towns of Fine and Clifton of St. Lawrence County, New York. The portions of the forest on which plots for this study were located were logged and then burned over prior to 1912, the year the College of Forestry obtained possession. The original forest cover is believed to have been similar to that found on the adjacent unburned state-owned land, namely: a mixture of yellow birch (*Betula alleghaniensis* Britton), beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.), with a good representation of red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Eastern white pine (*Pinus strobus* L.), black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), balsam fir (*Abies balsamea* (L.) Mill.), and white ash (*Fraxinus americana* L.) occur as scattered individuals. Young (1934) reported on a rather extensive ecological study of the virgin forest of this locality. Second-growth seedling and sprout hardwoods developed after the fire and these were removed during the period from 1933 to 1937. After clearing, conifers of several species were planted. The hardwood trees measured in this study have developed in the plantations after clearing.

Plot description

During the 1940 and 1942 growing seasons, the terminal elongation of several groups of small trees was measured at frequent intervals. In 1940, measurements were taken at three places designated as Plot A, Plot B, and the Frost Pocket. In 1942, measurements were taken on Plot B and on the Frost Pocket Plot and also on a new area designated as Plot C. For the purposes of this paper it is not important to distinguish between the various plots except to remember that Plots A, B, and C were approximately similar in relation to tree cover, climate, exposure, soil, and elevation. The Frost Pocket Plot was located in an area known to experience lower minimum air temperatures than the other plots and measurements were taken here to discover the effect of the lower temperatures on terminal elongation. These locations were selected because they provided one or more species of trees of small size which could be easily measured.

Methods

Selection of the trees to be measured

The individual sprouts or trees to be measured were selected in the spring before growth began, and were chosen so that, for at least one growing season, they would not experience serious competition with others around them. Trees whose tips were injured during the season were replaced by selecting another suitable tree in the vicinity. When the individuals to be measured during 1942 were selected, an attempt was made to use the same trees as were measured in 1940. Because of changes in competitive position and damage to growing tips, many of the trees which had been used two years before were judged unsatisfactory. So many tips of the Scotch pine in the Frost Pocket Plot were damaged that only six of the trees measured in 1940 could be measured again in 1942.

A tabulation of numbers of trees of each species measured each year on each plot is given in Table I. All of the hardwood trees measured were sprouts from the trees of the original forest cover, consequently, within species, they can be assumed to be genetically comparable. All of the conifers were planted. In the discussion of the data, when comparisons are made between groups of trees of the same species but differing in age or genetic origin, the points of dissimilarity will be mentioned.

Measurement of terminal elongation

Each selected tree was designated with a numbered wooden tag fastened to the tree with a fine copper wire. A fine steel pin was pushed through the stem of the tree to provide a point from which measurements could be taken. In conifers, the pin was placed near the terminal bud because the leader was large enough to contain it without danger of splitting, and the resin of the tree soon sealed the wound. In hardwoods, the pin was pressed through at a point some distance below the bud because the danger of splitting was greater. Hardwood stems which were split by the pins were abandoned. In 1942, white paint was used to mark a point on the stem of each hardwood tree in order to avoid any possibility of injury to the stem which might affect the rate of growth. The paint had to be renewed during the season and did not provide as definite a point

TABLE I. *Numbers of trees measured on each plot*

Species	1940			1942		
	Plot A	Plot B	Frost pocket	Plot B	Plot C	Frost pocket
Scotch pine (*Pinus sylvestris* L.)	30	0	25	0	33	30
Norway spruce (*Picea abies* (L.) Karst.)	13	25	0	25	0	0
Red pine (*Pinus resinosa* Ait.)	0	25	0	20	0	0
Austrian pine (*Pinus nigra* Arnold)	0	0	0	0	10	0
Eastern white pine (*Pinus strobus* L.)	0	0	0	15	0	0
Sugar maple (*Acer saccharum* Marsh.)	25	25	0	0	0	0
Red maple (*Acer rubrum* L.)	25	25	0	25	50	0
Black cherry (*Prunus serotina* Ehrh.)	25	12	0	0	0	0

from which measurements could be started as did the steel pin.

Measurement of the terminal elongation was accomplished by slipping the loop of a light steel tape over the pin and raising the tape until it could be sighted across the top of the terminal bud. In cases where the terminal bud was higher than the eye of the observer, the tree was bent by grasping it below the pin and pulling it toward the observer until the sight could be made. Care was taken not to injure the terminal buds or the leaves below the buds. This procedure is a modification of the general methods used by Hiley and Cuncliffe (1922, 1923), Kienholz (1932, 1934), Reed (1939), and Fowells (1941).

The tape was graduated to hundredths of feet and the measurement was estimated to thousandths of feet. Check measurements, made at various times, indicated that the actual measurements varied as much as three thousandths when the top of the bud could be seen. For a part of the period of most rapid growth, the top of the terminal bud could not be seen without pushing the newly formed leaves or needles to one side. This action would surely have caused some damage to the shoot and for that reason was not practiced. Probably some inaccuracy of measurements resulted from this, but there seemed to be no way of avoiding both damage and inaccuracy.

In 1940, measurements were taken at two-day intervals before and during the period of most rapid elongation. After the growth rate decreased, the interval between measurements was increased gradually until growth stopped. The measurements on Plot A were not taken on the same day as on Plot B. This proved to be undesirable when comparing growth curves of the same species on the two plots. In 1942, measurements were made daily for a 40-day period during the time of most rapid growth. Early in the season and after the period of most rapid growth, the measurements were taken at two-day intervals. In the course of the study, approximately 25,000 individual height-growth measurements were made.

Measurement of environmental factors

Measurement of some of the physical site factors were taken at each plot during the period of terminal growth. Instruments were established at Plots A, B, and C, and observations of air temperature, soil temperature, and evaporation were made each day. Soil moisture measurements were taken at intervals to insure the detection of periods of deficient soil moisture. The State Ranger School maintains a weather station at the Frost Pocket Plot in connection with one of its research projects, at which daily readings are taken by an employee of the school. The readings from this station were used for the Frost Pocket Plot.

For the measurement of air temperature, standard Weather Bureau type maximum and minimum recording thermometers were exposed in a standard type shelter with the thermometers at a height of 4.5 feet from the ground. Readings of maximum, minimum, and current air temperatures were taken at 5 P.M. each day and the thermometers were reset.

To obtain soil temperature data, thermometers were exposed at one inch, six inches, and twelve inches below the surface. Wooden soil tubes were prepared for the six and twelve inch depths. The third thermometer was placed with its bulb at a depth of one inch and read in place. These thermometers were read at 5:00 P.M. each day.

Soil moisture measurements were taken according to the methods of Bouyoucos and Mick (1940). Five plaster-of-Paris blocks were established in the soil at each plot. One was placed at one inch below the surface, three were distributed at the six inch depth and one was placed at the twelve inch depth. Resistance readings were taken at sufficiently frequent intervals to insure the discovery of periods of deficient soil moisture. The Bouyoucos and Mick method indicates moisture contents approaching the wilting percentage by readings of from 60,000 to 70,000 ohms resistance. Readings of this magnitude were not reached during the period of this investigation.

Evaporation data were obtained by exposing standardized black and white atmometer bulbs at 4.5 feet above the ground. This height, the same as that of the air temperature thermometers, exposed the bulbs to freely moving air and direct sunlight. The bulbs were not shaded by the vegetation except for short periods after sunrise and before sunset. An exception to this existed at the

Frost Pocket where the bulbs were exposed at a height of 10 inches from the ground. This is in accordance with the practice followed on all stations maintained by the Ranger School. The evaporation data from the Frost Pocket are therefore not comparable with those taken on Plots A, B, and C. However, they do indicate relative changes from day to day on the Frost Pocket Plot.

During 1940, an extra set of black and white bulbs were set up and used to check the evaporation of the regular bulbs. All bulbs were returned to Dr. Livingston in the fall of 1940 to be restandardized and were then used again in 1942. The instructions of Livingston (1935) and Stickel (1931) were of considerable assistance in operating the atmometers.

Discussion of Data[2]

At the end of each growing season, the growth data were summarized by species to obtain the average daily elongation per tree in thousandths of feet. The per cent of seasonal growth occurring each day was also calculated. These data are not valid for each day except when measurements of the elongation were made daily, and study of the figures disclosed that there was frequently a lag in response so that the effect of a change in temperature or other site factor was not well-expressed on the day it occurred. Accordingly, five-day moving averages of all growth and weather data were calculated, and comparisons among species, among plots, between years, and with site factors were made on this basis.

Terminal elongation

Figure 1 graphically presents the data on terminal elongation of several of the species studied through the growing season, compared with temperature and solar radiation. As mentioned above, all data are expressed as daily per cent of seasonal growth. The area under each growth curve therefore equals 100 per cent, regardless of the actual elongation in feet.

Curves of air temperature and of solar radiation (obtained from black and white atmometer bulbs) are shown for 1940 and 1942, and the curves are arranged so as to facilitate comparisons among plots for the same year, and for different years. When the relationships between elongation and air temperature and between elongation and solar radiation were studied, it became obvious that the elongation curves agreed much more closely with the curves of air temperature than with the curves of solar radiation. In the following discussion therefore, reference is made mostly to the air temperature curves and to their relationships with the elongation curves.

The curves of elongation were numbered to simplify reference to them. Curves 1, 2, 5, 6, 7, and 9 were plotted from data collected in 1940. Curves numbered 3, 4, 8, 10, 11 and 12 were plotted from 1942 data. The curves for red maple were all placed one above another, as were those for sugar maple and for Scotch pine, so that comparisons within species and between years could be made easily.

Considering for the moment only the 1940 curves, curves 1 and 2 were obtained for two groups of genetically similar trees growing on two separate but similar plots. The curves are very much alike in almost all respects. The dates of beginning and ending of elongation, the periods of increasing and decreasing rates of growth, the relative heights of the various parts of the curves, and the dates of maximum elongation all agree closely. They indicate a consistent response to variation in site factors by two independent groups of trees. Consequently, they demonstrate that such tree groups react alike. Incidentally, the agreement of the curves serve as a check on the methods of taking the field measurements, and on the methods of summarizing the data.

The curves for the other species prepared from 1940 data are similar to those for red maple in gross form only. They differ in degree of response, in length of growing period, in time of reaching maximum elongation and in other ways, so that the curve for each species is unlike the curve for each other species. As was true for red maple, however, the two curves for sugar maple agree very closely one with the other.

Shifting attention to the curves drawn from the 1942 data, the same generalities can be observed as for the 1940 data curves. Curves 3 and 4 for red maple are similar in almost every respect, and these are unlike the curves prepared for other species for the same season. Greater differences are evident between the curves for the various species for this season than between the species curves for the 1940 season. Examples of quite different response for two groups of trees of different species are provided by the Norway spruce of curve 10 and the white pine of curve 12. These trees were growing intermingled on the same plot so that site differences could not account for the differences in response. It is thus evident that species

[2] Although soil temperature and soil moisture measurements were taken they are not presented in this paper. The soil moisture did not approach the wilting percentage during the two growing seasons studied, consequently, variations in soil moisture were assumed to be but remotely related to variations in elongation. The soil temperature data are not presented because they are not as closely related to elongation as air temperature.

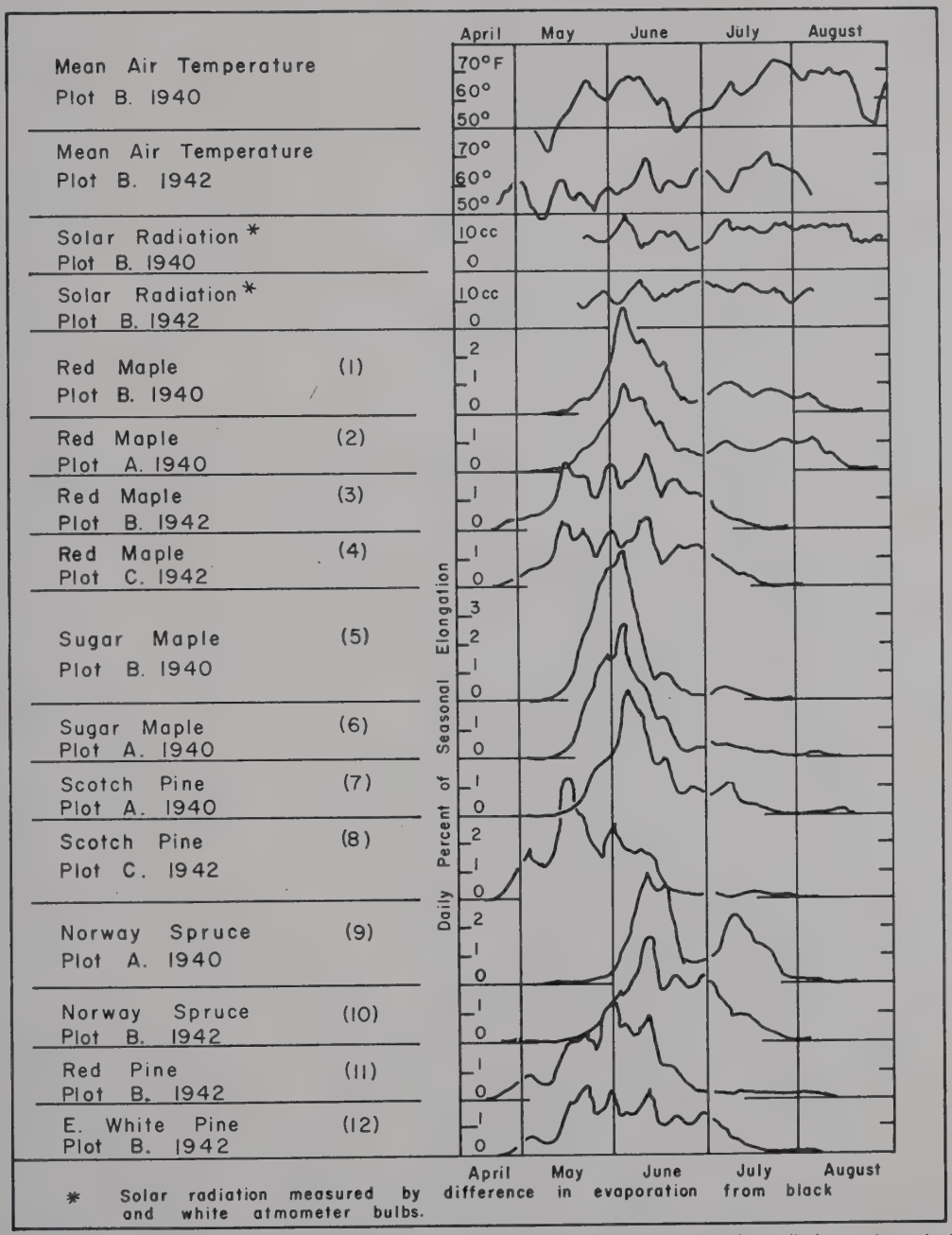

FIG. 1. Comparison of five-day moving averages for daily mean air temperature, solar radiation, and terminal elongation.

may express growth responses that are characteristic for the species and which are more or less different than the responses of other species growing on the same site.

In the above discussion, it has been pointed out that the curves for the same species during the same year are very similar. Curves for different species during the same year are unlike. It is interesting also to compare the curves for the same species on the same plot obtained for each

of the two growing seasons. Perhaps the most striking contrast is provided by comparing curves 1 and 2, with curves 3 and 4, all for red maple. Curves 1 and 2 are for 1940 data and 3 and 4 are for 1942 data. As mentioned above, the red maple sprouts grew from the original forest, and consequently are genetically comparable. Growth started earlier and ended earlier in 1942 than in 1940. There were three major maxima in 1942 compared with one in 1940. The general form of the curves from 1942 data resemble an irregular saw-tooth form, in contrast to the much more triangular form of the curve from 1940 data. There is little agreement regarding the dates on which growth trends changed sharply.

Curves 7 and 8 for Scotch pine, and curves 9 and 10 for Norway spruce also provide an opportunity to compare the growth curves of the same species during different years. The Scotch pine curves are very unlike. The Norway spruce curves are much more similar, however, there are many differences that can be easily observed. For these curves, however, it cannot be assumed that groups of the same species have the same genetic makeup. Although the two groups of Scotch pine are phenotypically similar, the records of origin are not sufficiently complete to assure that they are genetically comparable. The same reservation must also be made regarding the Norway spruce. In addition, there was a difference of 14 years in the age of the Norway spruce trees of one plot as compared with the other. The trees on Plot A were planted in 1921, those on Plot B in 1935. In spite of the difference in age, the trees were of about the same size due to hardwood competition during the period 1921-1934.

From the above, it can be generalized that terminal elongation curves for the same species growing on similar sites are very much alike during the same year. Curves for different species are unlike, and curves for the same species during different years are unlike. Data are available for but two growing seasons, and the number of trees and the size of the trees are small, therefore it is not appropriate to make generalizations beyond the data.

In studying the responses of all the species to changes in air temperature and other factors, it was obvious that there was relatively great response during the period of rapid growth and relatively less response either earlier or later in the growing season. If levels of air temperature and other site factors had been reached each day that was favorable for elongation, it is probable that the great curve of growth described by Illick (1919) would have been more clearly demonstrated.

The forms of the terminal elongation curves shown in Figure 1 are apparently the results of the physiological growth tendencies of the species, influenced by the intensity of the site factors. The strength of the tendency of a species to elongate according to a pattern that is characteristic for that species is not known. However, in the curves shown, it is apparent that factors other than those associated with the site are acting to partially determine the form of the curves.

The differences in degree of response to the intensity of the site factors shown by two species growing on the same site is sometimes pronounced and merits additional comment. Another example of this is provided by the curves for Norway spruce and red pine on Plot B during 1942 (Curves 10 and 11 in Figure 1.). These curves should be compared with the 1942 curve for air temperature to observe that they agree rather well concerning the dates on which changes of trend take place. It can be seen that in spite of points of similarity however, each is different from the other two in many respects. The red pine began elongation at an earlier date than the Norway spruce, and increased its rate of elongation in apparent response to the increase in temperature during the latter part of April. The Norway spruce grew very little during this period, and if there was a response to the increase in temperature it was too small to be detected. The red pine reacted sharply to the two periods of increasing temperature culminating approximately on May 15 and June 1, while the Norway spruce steadily increased its rate of growth during this period. However, the spruce showed a greater response than the red pine to the period of increasing temperature which reached its culmination about June 10. As a matter of fact, the spruce reached its highest rate of growth at this point. The red pine growth had passed its highest point on that date and did not react as strongly as did the spruce. The red pine did not show strong response to variations in air temperature after the middle of June and the rate of elongation decreased. The Norway spruce reacted quite strongly to two later periods of increasing temperature during June and then its rate of elongation gradually declined. Both groups of trees reached 99 per cent of their seasonal elongation on the same date (July 25). These two groups of trees were also intermixed on the same plot, so it can be assumed that both were subjected to the same intensity of site factors. They reacted differently due to species differences.

Even for species beginning and ending elongation at approximately the same time, as for example the Scotch pine and red maple on Plot C during the 1942 growing season, the form of the

elongation curves (Curves 4 and 8) may be quite different, due to differences in response during the growing season. Such differences are easily observed for the species mentioned. For other curves shown in Figure 1 there is less variation between the growth patterns for groups of trees of the same species growing on different plots during the same year than between the growth patterns of groups of trees of the same species growing on the same plot during two different years.

It is probable that the marked differences between the curves for the 1942 growing season and those for the 1940 growing season for a single species can be partially explained by referring to the air temperature curves for the two growing seasons. Probably the period of low temperature early in May of 1940 prevented rapid elongation from taking place. This did not greatly influence the development of Norway spruce because it apparently was not able to begin its rapid growth, but other species did not begin to elongate as early as they did in 1942 when higher early May temperatures occurred. Following the cool period in May 1940, the air temperature increased and was maintained at a relatively high level. The average mean daily air temperature for Plot B from May 20 to June 10 inclusive was 65° F. as compared with an average daily mean temperature of 58° F. for the same period and same plot in 1942. The higher air temperature presumably stimulated the trees to elongate at a more rapid rate than was the case in 1942, giving rise to the relatively steep and uniform increase prior to culmination. On June 10, 1940 the air temperature curve began to fall. All the species curves, except that for Norway spruce, showed culminations previous to June 6. The Norway spruce culmination occurred at about the time the air temperature began to decrease. The air temperature curve decreased until June 22, and then started to increase. All of the 1940 elongation curves showed the retarding effect of the air temperature decrease, and sugar maple (curves 5 and 6) did not increase in rate of elongation very much above that shown on the date of the lowest point of the air temperature curve. All of the others, and especially Norway spruce, increased their rates of elongation following the cool period and continued to grow for a considerable time. The low temperature periods of early May and late June 1940, with the high temperature periods following each, apparently provide an explanation for the form taken by the the elongation curves for that year. This pronounced sequence of temperature did not occur in 1942.

Length of apical growth period

The data obtained in the study of terminal elongation provided an opportunity to determine the beginning and the end of the apical growth period. Individuals of the same species of tree growing on the same plot showed variation in the dates on which they started and ended their elongation. This difference was as great as ten days at the beginning of the season, and as great as thirty days at the end, in trees which were apparently healthy. Generally, the larger individuals started earlier, grew faster, and stopped at a later date than the smaller individuals, but this was not always found to be true. Because of the variation among individuals, the growing period of the apical meristem was assumed to start on the day the average of the group of trees measured reached 1 per cent of the total elongation for the season. These limits were used by Baldwin (1931) for a similar purpose.

The dates of the beginning and ending of the growing season and the total number of days between these dates are provided by Table II, for each species on each plot. Also provided are the dates of the beginning and the end, and the number of days required for the measured trees to elongate the 50 per cent of the total elongation which occupied the shortest period of time. In case two or more combinations of dates indicated the same length of period for the occurrence of the most rapid 50 per cent of the elongation, the period nearest the beginning of the growing season was selected. It is interesting to compare the number of days required for the most rapid 50 per cent of the seasonal terminal elongation with the number of days required for the 1 per cent to 99 per cent of the total for the season. The ratios of the 50 per cent of total elongation to the 98 per cent of total elongation vary from 17 per cent to 37 per cent. They appear to be fairly consistent for the same species on different plots during the same year, but differ considerably in 1942 as compared with 1940.

The length of the apical growing period tended to be somewhat longer in 1940 than in 1942, although this was not pronounced except for red maple. The range in length of growing period shown by groups of red maple over both years was from a minimum of 76 days to a maximum of 101 days. For Scotch pine data from two plots for each of two years provided lengths of growing season of 84, 84, 85 and 87 days, and Norway spruce on Plot B during 1940 and 1942 indicated lengths of 71 and 74. From the data provided, it appears that conifers are much more consistent in length of growing period than hardwoods, but any

TABLE II. *Length of growing period and amount of apical growth*

Species	Year	Plot	Length of period required for 1% to 99% of total apical growth			Length of period required for most rapid 50% of total apical growth			Average total apical growth per tree (in feet)
			1% Date	99% Date	Total number of days	Beginning date and % of growth to date	Ending date and % of growth to date	Number of days	
Red maple	1942	B	Apr. 27	July 11	76	May 15 (15.56%)	June 11 (64.70%)	28	1.177
Red maple	1942	C	Apr. 28	July 19	83	May 13 (11.72%)	June 11 (63.06%)	30	2.112
Red maple	1940	B	May 6	Aug. 10	97	May 31 (12.97%)	June 20 (63.64%)	21	1.252
Red maple	1940	A	May 5	Aug. 13	101	May 28 (9.78%)	June 25 (59.98%)	29	1.673
Scotch pine	1942	Fr. Pocket	Apr. 27	July 22	87	May 14 (9.42%)	June 6 (58.23%)	24	.961
Scotch pine	1942	C	Apr. 25	July 18	84	May 12 (21.28%)	May 30 (71.91%)	19	1.360
Scotch pine	1940	Fr. Pocket	May 17	Aug. 9	85	May 30 (8.60%)	June 13 (59.07%)	15	1.309
Scotch pine	1940	A	May 11	Aug. 2	84	May 27 (12.68%)	June 12 (62.85%)	17	1.913
Red pine	1942	B	Apr. 25	July 25	86	May 23 (31.86%)	June 12 (81.26%)	21	1.199
Red pine	1940	B	May 9	Aug. 4	88	May 30 (14.53%)	June 13 (64.12%)	15	1.084
Sugar maple	1940	A	May 13	Aug. 3	83	May 22 (8.52%)	June 5 (57.83%)	15	1.588
Sugar maple	1940	B	May 12	July 12	62	May 21 (9.47%)	June 3 (60.45%)	14	1.125
Nor. spruce	1942	B	May 16	July 25	71	June 3 (15.45%)	June 24 (65.22%)	22	1.226
Nor. spruce	1940	B	May 20	Aug. 1	74	June 3 (5.61%)	June 20 (55.74%)	18	.832
Nor. spruce*	1940	A	May 31	Aug. 2	64	June 3 (4.23%)	June 19 (54.08%)	17	.920
Bl. cherry	1940	A	May 5	Aug. 1	89	May 25 (21.62%)	June 13 (71.23%)	20	1.056
Bl. cherry	1940	B	May 7	July 12	67	May 20 (10.67%)	June 5 (59.81%)	17	.854
Austr. pine	1942	C	Apr. 28	July 25	89	May 27 (23.87%)	June 17 (73.70%)	22	1.200
E. white pine	1942	B	Apr. 28	July 19	83	May 17 (16.46%)	June 13 (66.85%)	28	1.593

*Data for Norway spruce Plot A, 1940 are not strictly comparable, because measurements were not started until elongation was underway. The beginning of elongation was not determined.

attempt to fix a length of growing period which would be characteristic of a particular species was not practical.

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AN ECOLOGICAL STUDY OF THE BEHAVIOR OF THE LEAF-CUTTING ANT *ATTA CEPHALOTES*[1]

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Tropical environments are generally characterized by a fauna comprising numerous intensely competitive species, with no one type predominant (Dobzhansky 1950). Special interest is therefore attached to the factors responsible for the biological success of animal types that are unusually abundant and have become established in a wide variety of tropical habitats. On the basis of these criteria, the fungus-growing ants have been considered the dominant invertebrates of tropical America (Wheeler 1907). Fundamentally, the prominence of the Attine ants in the tropics results from the fact that they have evolved physiological mechanisms which operate to produce a behavioral pattern resulting in the tapping of a virtually inexhaustable food supply. The operation and evolution of the physiological mechanisms underlying this behavior have been little studied although their investigation might reveal some of the neurological factors concerned in the evolution of a group of animals among which behavioral patterns are of extraordinary importance.

Goetsch (1939) demonstrated that the foraging trails are chemically polarized, and that the "light compass" reaction could also be employed in orientation, although the latter mechanism may be absent among forest-dwelling species which are exposed to relatively dim and sporadically distributed illumination. The factors which determine the times when the animals are active, and hence the ecological conditions to which they are exposed, have been discussed by Lutz (1929). He observed no activity outside the nest of *Atta cephalotes* before sunrise or after sunset, and concluded that light was the environmental variable which initiated and cut short the daily activity. However, other observers (Walcott 1933; Weber 1941, 1946) have found the same and closely related species of *Atta* active outside the nest at night in comparable habitats. Eidmann (1935) believed activity outside the nest to be related to temperature. It has also been suggested that the ants merely continue one activity until it is no longer possible to do so (Goetsch 1939). For example they might eat fungus within the nest until the supply becomes exhausted.

The factors initiating and terminating activities outside the nest constitute a logical starting point for an investigation of the physiological mechanisms underlying the diverse behavior patterns of adaptive significance throughout this group of animals. At the present time there appears to be no adequate basis for choosing between such alternatives as a controlling internal rhythm, dependence on stimuli of light, humidity, or temperature, regulation according to the condition of the fungus gardens, or combinations of these factors. In addition to defining the stimuli prerequisite for their activities, such information is necessary to discover the actual range of ecological fluctuations in which the species lives within the larger range of ecological fluctuations occurring in its geographical range. Allee (1926) has shown that even the relatively equable environment under the rain forest canopy exhibits rhythmic fluctations in temperature, evaporation rate, etc., and the particular conditions which a species encounters, and possibly the conditions which it can tolerate, cannot be determined without knowing when the animals are active outside the more constant conditions which presumably prevail in the nest. It is the aim of the present study to determine major environmental variables encountered by a typical rain-forest species of fungus-growing ant and the manner in which the activities of the species are influenced by these factors.

MATERIALS AND METHODS

The large leaf-cutting ant, *Atta cephalotes* L. var. *isthmicola* Weber, was the species studied. This species includes the most conspicuous of the Attini living in the northern half of the continental New World Tropics (Weber 1941). The study was conducted on ants having a nest located 150 meters from the edge of the clearing which surrounds the laboratory of the Institute for Research in Tropical America on Barro Colorado Island in the Panama Canal Zone. Ventilation and exit holes of this nest covered an approximately circular area which varied from 12 to 14 meters in diameter. The presence of approximately 400 holes in the nest indicated that the colony

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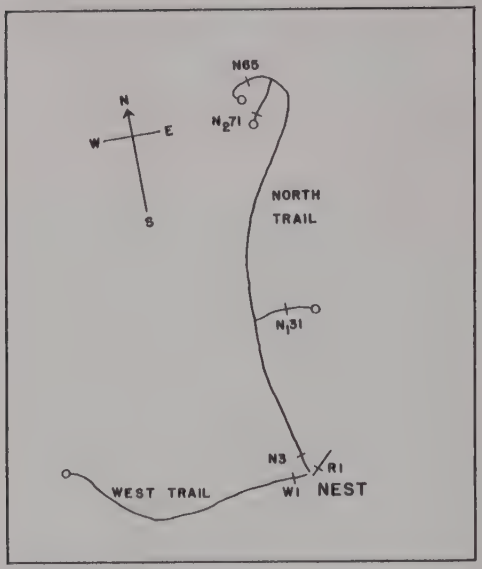

FIG. 1. Map of foraging and refuse trails of colony studied. Scale: ½ inch = 10 meters. For explanation of symbols, see text.

probably had not reached maximum size (Bitancourt 1951), but undoubtedly contained individuals representing all the different castes produced in the species.

The system of trails followed by the ants in their daily foraging activities is diagrammed in Figure 1. As is well known, the trails are cleared of all debris and may be easily traced along the forest floor, even when not in use by the ants. The trails were measured by laying a tapemeasure along the adjacent ground. Positions on the foraging trail are designated by a letter and a number. The letter indicates the compass direction toward which the trail extends from the nest, and the number is the distance in meters between the point at which the observations were made and the hole through which the trail passes into the nest. Branch trails are designated by subscripts. The trail over which refuse from the nest was carried to a dumping area is designated *R*. In addition to the two main foraging trails and the refuse trail, several small foraging trails were often found near the nest or branching from the ends of the main foraging trails. The course of these smaller trails was quite variable from day to day and the number of ants passing over them entirely negligible in proportion to the number using the trails shown in Figure 1. Additional small refuse trails were also present, but were likewise temporary and their use constituted a negligible part of the activity of this colony. Both the foraging trails and the refuse trail diagrammed in Figure 1 had been in use for at least seven months, as was noted by a comparison of an earlier mapping of the trail system with the present diagram.

To obtain a measurement of the relative use made of the various trails, the number of ants carrying pieces of leaves was counted at observation points located on the foraging trails and their major subdivisions. Counts were made during 5 separate intervals of 1 minute each near the height of the day's activity between 11:30 A.M. and noon. Data for two typical days are presented in Table I. Standard errors are rounded to the closest whole number. By comparing the data for the two days it can be seen that although the absolute numbers of foragers differs on the two days, the proportions of ants using the main and the subsidiary trails were not significantly different on the two days. This was true during the entire period of the study, from July 14 to August 23. Hence, from a measure of the activity over any one part of the trail system, a reasonable estimate for any other point could be made.

The activity at various hours was measured by counts of worker ants passing observation positions *W3, N3,* and *R1.* At positions *W3* and *N3,* the categories of ants passing were recorded in the following order: west trail outgoing (WO); west trail ingoing, laden with leaves (WL); west trail ingoing, unladen (WU); north trail outgoing (NO); north trail ingoing, laden with leaves (NL); north trail ingoing, unladen (NU). The sequence was concluded by a count of the outgoing refuse-carrying ants passing *R1.* This sequence was repeated 3 times so that the data were accumulated over a period of 21 minutes (plus the time necessary to move between counting positions) after the counts were begun. The average count for each category of foraging ant at the various trail positions is the value reported in the tables which follow.

Most of the temperature measurements were

TABLE I. *Relative use of trails and their subdivisions. (See text.)*

Date	No. ants/min. passing observation points ± st. error				
	W3	*N3*	*N65*	$N_1 31$	$N_2 71$
July 16.....	93±4	117±5	90±5	5±5	7±3
Aug. 23.....	164±18	152±20	111±9	12±6	10±4

made with mercury column thermometers, accurate within 0.25 degree C. The temperature reading taken inside the ant nest were made by introducing one temperature sensitive element of a Taylor Indoor-Outdoor thermometer into one of the exit holes of the nest. In this way, the temperature was measured at a point two feet from the opening of one of the tunnels used as an entrance by the foraging ants. The temperature was measured approximately one foot under the surface of the ground inside the nest. The Taylor thermometer was calibrated with the mercury column instruments.

Relative humidity was measured by means of a Weston humidograph, accurate within 1% relative humidity, and light intensities were measured by a General Electric PR-1 Exposure Meter, the calibration of which was kindly supplied by the Meter and Instrument Division of the General Electric Company. The microammeter of this light meter has equal accuracy at all the light values recorded. Since the amount of light reaching different areas of the forest floor was very unequal because of shadows from the forest canopy, the brightest light reaching any part of the nest site was recorded as the intensity of light at any particular time of day. These values represent the maximum illumination to which the ants were exposed at the entrances to the nest or on their foraging trails. Minimum illumination on the forest floor varied from zero to approximately 10 foot-candles during the brightest parts of the day. Other procedures and equipment are described at appropriate points below.

Results

From the beginning of the observations, it became apparent that there was no single rhythm of activity which applied to all the individual ants working outside the nest. There were, in fact, two separate types of activity which operated independently outside the nest. Certainly they are initiated and carried on as a result of reactions to different stimuli. They will be considered separately.

A. The diurnal foraging cycle

The most conspicuous activity of the larger species of fungus-growing ants consists in the foraging behavior. Briefly, the workers travel away from the nest, sometimes for several hundred meters, until they reach a food tree which they ascend. Semi-circular pieces are cut from the leaves of the tree by use of the mouthparts. The leaf fragments are carried in the jaws of the ant as it returns to the nest over the same trail. The events inside the nest, which include chewing of the leaf fragment and its eventual incorporation into the fungus garden, will not be of concern here. It would be expected, as will be definitely shown below, that the interior of the nest provides a much more constant environment than that found outside. It follows that if the foraging activity is not entirely dependent on an internal physiological rhythm, the most likely place to look for a controlling stimulus is outside the nest.

The foraging activities of the ants were measured, by the method outlined above, from July 14 to August 7, inclusive. During this period, there were only 4 days when the foraging activities of the ants were undisturbed by rain. The data collected on those 4 days are believed to represent the simplest pattern of foraging activity which occurs during the rainy season. No significant differences were found between the data obtained on July 14 and July 15, but both of these differed from the findings on July 19 and August 6. The data for July 15 and July 19 are representative of the two types of data and are presented in Table 2. The July 15 data are plotted graphically in Figure 2.

Comparison of these data reveals the following: (1) the over-all pattern of foraging activities is the same on both of the days used as examples, when the same trails are compared; (2) however, the time at which the foraging activities began differs significantly on the two days—being later on July 19 and, on both days, later on the west trail; (3) the pattern of activities on both trails, once initiated, seems to bear no relation to the fluctuation of light intensity, temperature, or humidity occurring between 7:00 A.M. and 4:00 P.M.; (4) regardless of the time at which the foraging pattern was initiated, the activity stops at about the same time.

In attempting to discover the important environmental fluctuations to which the ants are responding, any such variables occurring between the onset and the cessation of foraging activities may be reasonably ignored, inasmuch as the foraging cycle follows its own characteristic pattern despite the different conditions at comparable hours on the two days. For each of the two days used as examples, and in the two others which resemble them, this characteristic pattern includes the following: (1) a peak in the number of outgoing workers at about two hours after the start of the daily cycle, and a gradual decline in numbers of ants in this category until an abrupt termination of activities in late afternoon; (2) a gradual increase in the number of ingoing laden work-

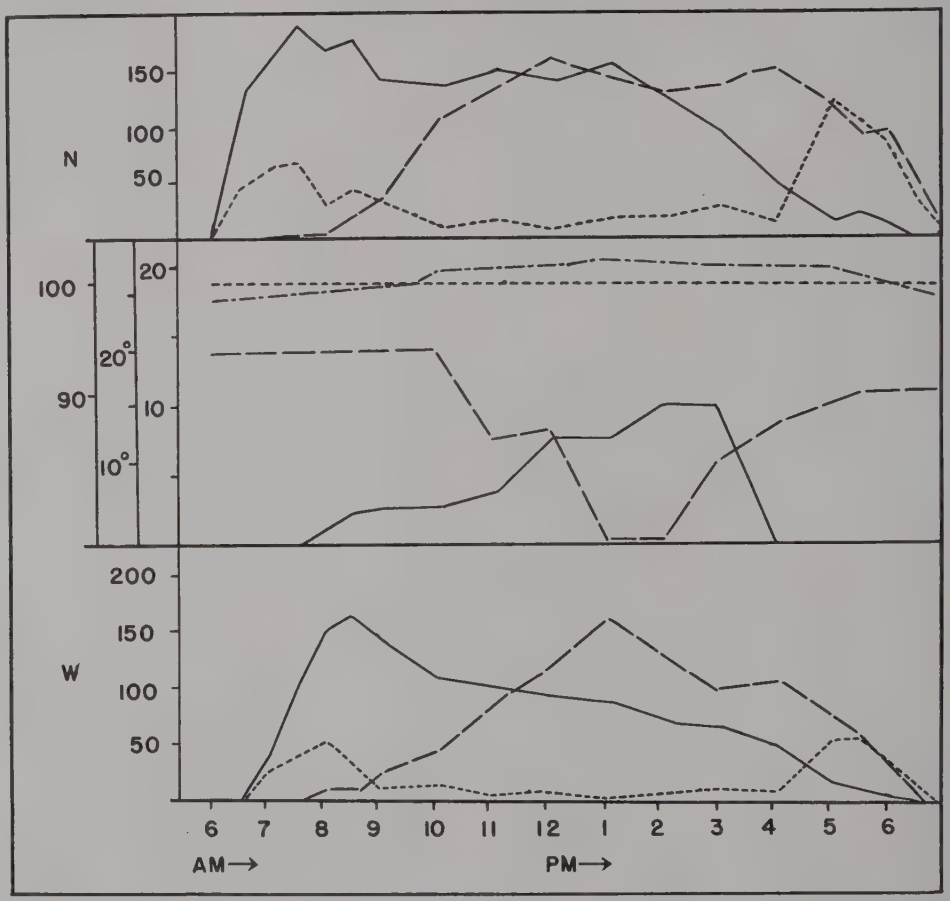

FIG. 2. Ecological data and activity pattern on July 15. The upper and lower sections of the graph show the patterns of activity on the north and west foraging trails, respectively. In these sections, the solid lines represent numbers of outgoing workers; dashes, ingoing laden workers; dots, ingoing unladen workers. The ordinates of the upper and lower sections indicate the number of ants counted at positions N_3 and W_1, respectively. The ordinates of the center section indicate, reading from left to right: percentage relative humidity, degrees centigrade, and thousands of foot-candles. In the center section the solid line indicates the intensity of illumination; dashes, relative humidity; dots, temperature inside nest; alternate dots and dashes, outside temperature. The abscissa indicates hours of the day for all three sections of the graph.

ers to a peak around noon, and a slow decline in their numbers beginning in mid-afternoon and continuing until all activity outside the nest ceased; (3) a large number of ingoing unladen workers during the two-hour period following the start of activities and during a comparable period before activity ceased.

The amount of light reaching the forest floor is the only factor measured which shows a correlation with any part of the foraging cycle. Though the scale of the plot in Figure 2 is of necessity such that differences in very low light intensities are not shown, the data presented in Table II show that in none of these cases did the ants leave the nest before light with an intensity of approximately 0.3 foot-candles falls on the nest. This suggests that the initial egress from the nest occurs in response to a definite intensity of light. This possibility is strengthened by the difference between the onset of activities on the north and west trails. The first two and one-half meters of the west trail were in a sheltered position, passing under a root adjoining the nest. The north trail was in a position exposed to the first light entering the forest. By measuring the intensity of light reaching the nest openings of the north and west

TABLE II. *Ecological data and activity pattern on July 15 (upper figures of each set) and July 19 (lower figures). Temperature is expressed in degrees centigrade, light in thousands of foot-candles. Symbols are explained in text.*

Time	Temperature		Relative humidity	Light	WO	WL	WU	NO	NL	NU	R
	Inside nest	Outside nest									
6:00 A.M.	26	24.7	93	0	0	0	0	0	0	0	97
	26	26.1	85	0	0	0	0	0	0	0	104
6:15	26	24.7	..	0.3	0	0	0	64	0	28	95
	26	26.1	..	0	0	0	0	0	0	0	100
6:30	26	24.7	93	0.6	0	0	0	120	0	43	101
	26	26.1	85	0	0	0	0	0	0	0	102
7:00	26	25.0	..	4	36	0	27	153	0	62	89
	26	26.1	..	1.2	0	0	0	20	0	10	110
7:30	26	25.1	94	160	100	0	41	189	0	66	97
	26	26.1	85	4	0	0	0	56	0	25	100
8:00	26	25.5	94	1,400	152	9	59	168	4	34	104
	26	26.4	86	12	41	0	19	116	0	51	108
8:30	26	25.5	94	2,330	166	11	30	177	20	41	95
	26	26.4	86	25	133	0	55	160	1	70	101
9:00	26	25.6	94	2,800	143	24	17	140	35	33	99
	26	27.0	87	130	159	30	25	151	0	45	107
10:00	26	27.0	94	2,800	110	47	18	136	103	14	107
	26	27.5	80	3,300	169	70	12	129	45	18	112
11:00	26	27.5	86	3,800	98	88	6	148	132	16	90
	26.5	28.0	80	3,300	110	103	11	130	106	19	103
12:00	26.5	27.5	87	7,600	95	121	9	140	157	10	98
	26.5	28.5	75	8.800	84	115	17	112	139	4	114
1:00 P.M.	26.5	28.3	78	7,600	89	164	4	156	145	19	100
	26.5	29.0	71	7,600	60	152	8	87	120	9	111
2:00	26.5	28.0	77	10,066	71	130	11	128	130	22	87
	26.5	29.0	76	7,600	54	128	14	90	141	15	100
3:00	26.5	27.5	84	10,066	66	104	10	99	135	34	96
	25.5	28.3	81	7,600	44	119	5	75	139	15	107
4:00	26	27.5	87	1,900	51	109	10	51	148	16	95
	26	28.0	89	3,800	22	89	6	60	122	19	113
5:00	26	27.5	89	3	11	75	49	19	120	120	99
	26	27.0	89	1,400	8	80	28	28	96	59	98
5:30	26	26.5	89	1.2	6	62	56	23	94	111	102
	26	27.0	89	2.5	1	33	63	30	85	75	108
6:00	26	26.0	89	0	1	31	40	15	98	89	91
	26	26.4	88	0.6	2	4	31	2	62	50	104
6:30	26	25.0	89	0	0	7	2	2	57	35	95
	26	26.4	89	0	0	10	8	5	33	40	104
7:00	26	25.0	89	0	3	0	0	4	14	1	85
	26	26.4	89	0	0	11	0	2	20	0	112
7:30	26	25.0	89	0	0	0	1	0	21	0	102
	26	26.1	88	0	0	0	0	0	11	0	101

trails, it was found that shortly after sunrise, when 0.3 foot candles or more could be detected at the opening of the north trail, no light could be detected at the opening of the west trail. This explains the later beginning of foraging on the west trail.

If considerable numbers of the ants respond to such a small amount of light, there must be a mechanism for bringing them to the opening of the nest before the time the first light reaches the forest floor. During the night, no ants were observed on the foraging trails or in the nest immediately inside the openings of the trails. About an hour before dawn, the workers could be seen moving inside the opening of the nest, although they did not leave the nest at that time. A flashlight covered with red cellophane was used for these observations and no change in the behavior of the ants was observed as a result of their brief exposure to dim red light, to which they would presumably be relatively insensitive (Dethier 1953). The movement of ants to the vicinity of the nest opening before dawn indicates an inherent diurnal rhythm, quite apart from the effects of light or any other variable operating outside the nest.

The postulated operation of light in conjunction with an inherent rhythm is experimentally testable by exposing the ants to light when no such stimulus would normally be present. The presence of two trails from the same nest, one trail suitable for use as a control for the experimental conditions imposed on the other, provided a convenient arrangement for carrying out this experiment.

Two experiments were performed, each in duplicate. To test the positive effect of light, a gasoline lantern was suspended two meters from the entrance of the west trail into the nest, and placed in a position so that its light fell on the inside of the nest. The lantern was lit at 5:00 A.M., as the ants began to congregate in this area of the nest. The north trail was not illuminated and a screen of palm branches was set up to shield the north trail from the light. The illumination from the lantern measured 80-160 foot-candles around the entrance of the west trail into the nest. No attempt was made to determine the predominate wavelengths of the light from the lantern, since it sufficed to know that the ants were stimulated, although the proportion of the effective wavelengths would undoubtedly be quite different in a comparable total intensity of sunlight. The results of this experiment are shown in Table III. On both August 5 and August 6, the egress of workers first began on the west trail, and this was exactly the reverse of the normal situation in this particular colony. No temperature change was detected just inside the point of entrance of the west trail into the nest during this experiment. The normal pattern of morning activity was observed on both trails on days before and after these data were collected, so the experiment definitely did not involve a chance atypical behavior pattern.

TABLE III. *Effect of light on initiation of foraging. Symbols are explained in text.*

A. Experimental illumination of west trail.

Time	August 5		August 6	
	NTO	WTO	NTO	WTO
5:00 A.M.	0	0	0	15
5:10	0	2	0	19
5:20	0	27	0	54
5:30	0	90	0	111
5:40	0	87	0	87
5:50	0	103	0	99
6:00	0	105	0	100
6:15	0	96	0	100
6:30	42	109	8	97

B. Experimental darkening of north trail.

Time	August 8		August 9	
	NTO	WTO	NTO	WTO
6:30 A.M.	0	66	0	0
6:40	0	80	0	52
6:50	0	120	0	69
7:00	0	136	0	92
7:10	0	118	0	90
7:20	0	121	0	90
7:30	0	108	0	99
7:40	4	123	0	125
7:50	12	139	0	118
8:00	8	130	2	107

In order to determine whether the ants could be stimulated to activity outside the nest during hours of the night when they were not active near the openings of the trails, the lantern was used on two other nights at 10:00 P.M., 1:00 A.M. and 3:00 A.M. Despite the fact that the brightest possible illumination was deliberately allowed to fall for as long as one-half hour on various exit and ventilation holes over the whole nest area, the results were entirely negative for no ants emerged onto the foraging trails. It was concluded that either the ants are insensitive to a stimulus normally effective, or (more likely) that they had all withdrawn to portions of the nest not reached by the light. This result also supports the hypothesis of a definite internal rhythm.

A converse type of experiment was performed to determine whether the ants would leave the nest

in the absence of light. This was done by draping opaque black cloth over U-shaped wickets placed over the north trail and completely covering the trail for three meters, as well as covering the junction of the trail and the nest. The end of this tunnel-like arrangement was closed so that no light could penetrate to the interior. This arrangement essentially duplicates that used in an experiment of Lutz (1929), and the results are in accord with his observations. As can be seen in Table III, the ants did not get to the usual counting position on the north trail (*N3*) until activity was well underway on the normally retarded west trail. The effect of the light shield in this case seems unequivocal. However, it is interesting to note that despite a delay, the ants eventually did push out under the cloth which closed the end of the tunnel. This demonstrated that the inherent activity of the ants is sufficient to bring about an exodus from the nest, but appears to do so at a much slower rate than when accelerated by reaction of the ants to light.

B. Influence of rain on the foraging cycle

The data presented thus far actually represent a situation which rarely occurs during the rainy season in the tropical rain forest. The variations from this simpler pattern of activities, however, can be accounted for in terms of the effects of the heavy rains which usually fall sometime during the day.

As soon as rain begins to fall on the trail, the ants, regardless of the direction in which they are moving or whether they are carrying leaves, begin to run toward the nest. The change of speed is obvious even when not timed, but speeds of 9.3 seconds for unladen ants to go one meter were observed just after the onset of rain, as opposed to 27.9 seconds to travel the same distance when undisturbed. The same effect can be obtained by blowing on the animals, though in this case the effect is momentary for they quickly move out of range of the stimulus. This reaction might result in the return of most of the ants to the nest in the case of a small colony. With a large colony, having extensive foraging trails, this is not true. From Table I it is apparent that most of the ants on the north trail, for example, would be beyond the junction of branch N_1 with the main trail and would require, even if unladen and proceeding with maximum speed, at least one-half minute to reach the nest. Actually, since the laden foragers move more slowly and obstacles and inclines in the trail also retard the ants, only a small fraction of the foraging ants reach the nest. After about one minute, the mechanical effects of the rain typically became so severe that the ants could not use the trails at all. The laden workers then drop their leaves and run until they reach a position where the rain no longer strikes them. It is common to find them clinging by the hundreds to the sheltered side of a tree buttress or root along the foraging trail. When the rain stops and the ants begin to move along the trail again, they still are exposed to dripping water from overhanging vegetation, and they appear to react to the dripping water in the same way as to the first drops of rain which fall, proceeding as rapidly as they can toward the nest. The dripping may persist as long as two hours with enough intensity to keep the ants moving toward the nest. The essential effect of rain, therefore, is the loss of an appreciable fraction of the day's foraging time.

The effects of rain on the diurnal foraging activities are of interest in providing a possible explanation for the foraging activity reported to occur during the evening and night. Data for a typical day, appropriate for analysis in this connection, are presented in Table IV and Figure 3. If the colony needed a certain total amount of leaf substrate for the fungus gardens every day, it would be expected that the interruption of foraging as a result of rain would lead to nocturnal continuation of foraging until the usual amount of substrate had been brought to the nest. The data show this hypothesis to be incorrect.

The record for this day, July 29, shows that 1.46 inches of rain fell between 12:05 P.M. and 2:50 P.M. The drip and runoff period following the rain continued for about 1½ hours, so that no foragers left the nest for more than 3 hours, during the time of day when the largest number of leaves would otherwise have been cut. The data in Table IV and Figure 3 cover only the period from 11:00 A.M. until cessation of activity, since the activity during the early part of the day was similar to other mornings without rain.

From a consideration of these data it is apparent that there is no significant prolongation of the time during which unladen foraging ants left the nest, for they stopped at approximately the same time as on days when there was no interruption of activity by rain. On the other hand, the gradual decline in the numbers of incoming foragers apparent on the rainless days does not occur, and a larger number of workers than would otherwise occur on the trails at that time of day was counted leaving the nest until the egress was halted by dim light. These observations can be interpreted according to the following conceptual scheme: (1) the decline in

TABLE IV. *Effect of rain on activity pattern. Symbols as in Table II.*

Time	Temperature		Relative humidity	Light	WO	WL	WU	NO	NL	NU	R
	Inside nest	Outside nest									
11:00 A.M...	26.3	28.2	96	350	143	114	11	150	130	0	93
12:00.....	26.3	28.2	96	3	155	110	7	148	139	4	87
	Rain										
3:00 P.M...	22.9	21.5	95	80	47	6	62	33	29	80	0
4:00.....	24.0	26.3	95	1,400	115	10	41	162	40	37	8
4:30.....	24.2	26.5	95	900	181	32	20	190	19	46	102
5:00.....	24.3	26.9	93	6	97	55	33	175	26	35	170
5:30.....	24.4	27.2	91	0.6	30	40	59	87	29	91	163
6:00.....	24.6	27.3	90	0	8	28	70	21	30	94	156
6:30.....	24.7	27.3	90	0	4	34	54	0	12	84	179
7:00.....	25.0	27.3	90	0	5	26	21	10	22	19	151
7:30.....	25.0	26.8	90	0	0	29	9	2	36	17	170
8:00.....	25.0	26.1	90	0	7	39	8	0	30	11	142
8:30.....	25.1	25.7	87	0	0	15	8	0	21	18	118
9:00.....	25.1	25.5	87	0	6	8	3	0	29	1	131
9:30.....	25.1	25.5	88	0	0	2	2	1	4	1	96
10:00.....	25.2	26.0	88	0	0	4	0	1	10	2	84
10:30.....	25.2	26.1	88	0	0	0	0	0	10	0	87
11:00.....	25.0	26.0	87	0	0	0	0	0	3	0	92

numbers of workers leaving the nest during late afternoon on rainless days results from the delay of workers in the nest chewing leaves, possibly eating as well; (2) under these conditions, a smaller number of ants is actually on the trails when the light intensity is no longer sufficient to stimulate unladen workers to leave the nest; (3) when the light intensity drops below approximately 3 foot-candles, the unladen workers no longer leave the nest and unladen workers on the trails start to return to the nest; (4) laden workers on the trail do not abandon leaves they are carrying, but proceed toward the nest more slowly than unladen workers when the light intensity drops below the critical intensity.

The operation of these processes would account for the appearance of greater activity outside the nest after the light intensity was zero on days when foraging was interrupted by rain. Large numbers of workers returning to the nest just after the rain starts and immediately after it stops result in a larger number of workers than would otherwise be the case leaving the nest following the drip and runoff period of the rain. Unfortunately, the egress of workers from the nest after rains, though it involves as many workers as the morning egress, does not commence as abruptly as when light first reaches the nest in the morning. Even when well underway, the movement of workers along the wet, debris-covered trail does not proceed smoothly, for temporary detours to standing water and other obstacles have to be made. Nor does this greater number of foragers leaving the nest compensate for the foraging time lost during the rain, for they cease activity at the same time as on rainless days, despite the fact that the laden ants may continue to come into the nest until 10:00 or 11:00 P.M. This prolongation of activity for this group of ants results from the facts that they do not release their leaves after dark, their progress toward the nest is normally slower than the unladen ants, and their progress over the rain-washed and debris-covered trail is even slower.

The number of unladen workers moving toward the nest is higher after the trail has been washed with rain, suggesting that this category of ants represents individuals temporarily disoriented from a weakened odor gradient. This hypothesis is supported by finding that both after rains and during the first hour after the morning egress the ingoing unladen ants proceed no more than a few meters toward the nest before reversing their direction. These cases of temporary disorientation are also more common near the edges of the trail where the olfactory stimulus would be expected to be weaker. This interpretation is in direct contrast to an interpretation of this activity by Lutz (1929), as will be mentioned in the discussion.

C. The pattern of activity in detritus removal

The second type of activity of the ants outside the nest consists of the removal of earth, used fungus substrate, dead ants, and miscellaneous other waste materials from the nest. This activity occurs independently of the foraging cycle as shown by the data presented in Tables II and

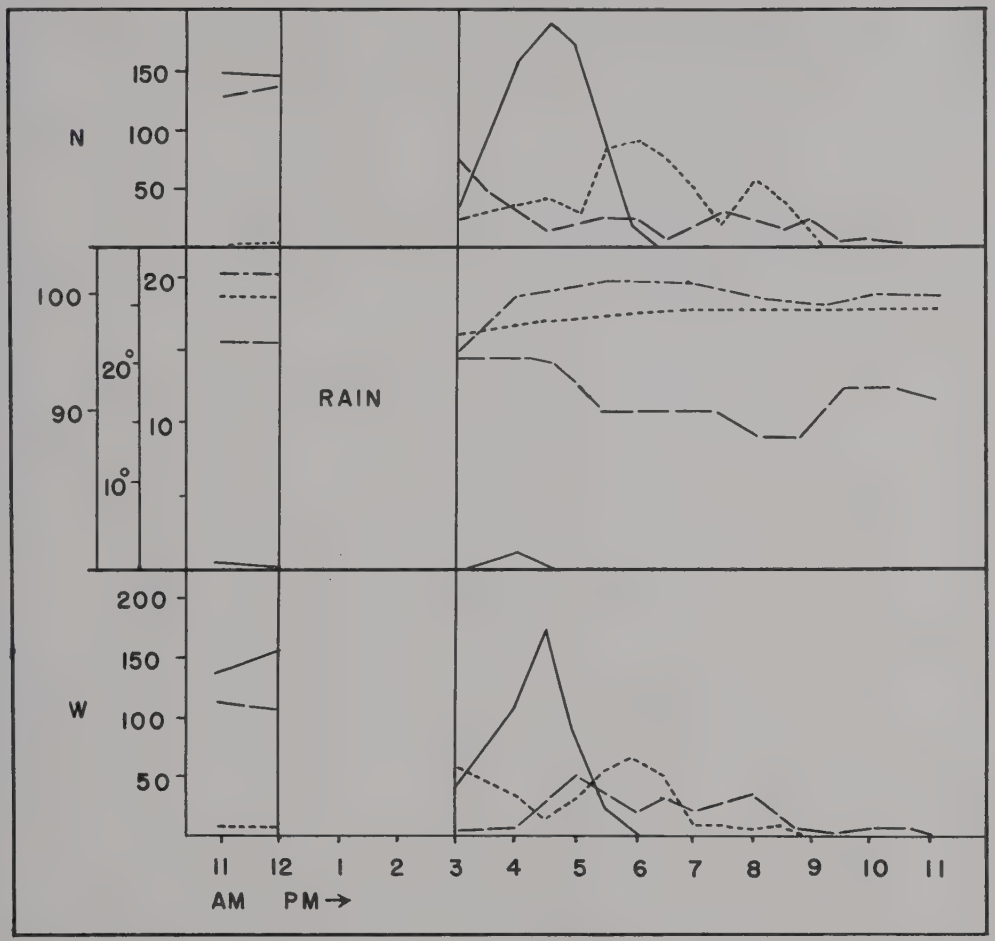

FIG. 3. Effect of rain on activity pattern. Ordinates and abscissa as in Figure 2.

IV. On rainless days, this activity continues at approximately the same rate throughout the period of daily observations. To determine whether the activity continued throughout the night, counts were made at 10:00 P.M., 1:00 A.M., and 3:00 A.M. on two nights. Since none of these data show any significant variation from those obtained during the day, these counts will not be added to those already presented. It is clear that the removal of detritus continues twenty-four hours a day, unless interrupted by rain. This activity is initiated and carried on as a result of different stimuli from the foraging activity, and no indication of an inherent rhythm was noted for it, although there may be slow fluctuations in the level of activity over longer periods of time.

Unlike the foraging cycle, there is a striking adjustment of the detritus-removal activities to the effects of rains. This can be seen in the data in Table IV. During the morning, an average of 90 ants/minute carried refuse from the nest along trail *R*. From 5:00 P.M. until 9:00 P.M., the number of ants carrying refuse averaged 66/minute higher than the morning average. While this does not compensate exactly for the stoppage of activity during four hours because of the rain, there seems little doubt that with the slow decline in the level of activity to the morning average, the increased activity following the rain approximately compensates for the effects of the rain. From this it seems probable that excavation within the nest is proceeding continuously and the detritus stimulates the workers which remove it very shortly after it is accumulated.

The seeming independence of foraging and detritus-removal activities from each other raises a question as to whether the same ants may participate in either type of activity in a mature

colony. No difference in total weights or proportions of body parts were found in ants taken from the refuse and foraging trails, and the question was settled conclusively by a marking experiment. Approximately 1000 refuse carriers were marked by applying a bright color of fingernail polish to their rear legs. This dried quickly and usually did not interfere with the activity of the ants. Many of these ants were subsequently found carrying refuse or being carried as refuse, but two of them were discovered bringing leaves to the nest over a foraging trail the day after marking. It can thus be concluded that although not necessarily a common occurrence, the same worker ant may engage in both types of activity, and the dissimilarity of the activity cycles lies in the nature of the process and not in the participating animals.

Discussion

The importance of light in controlling the foraging behavior of *A. cephalotes* resembles findings concerning several other animals, both invertebrates and vertebrates, inhabiting the rain-forest (Lutz 1931). The extensive studies of army ants (*cf.* the review of Schneira, 1953) have shown that the daily raids of terrestrial species begin at dawn and end at dusk, while the activities of the subterranean species are more irregular. *Atta* differs from the army ants, however, in lacking a midday lull in activity. The regularity with which the leaf-cutters leave their subterranean nest for foraging results from the additional process of an internal rhythm which brings worker ants to areas of the nest near the exit holes where they are exposed to the first light reaching the forest floor. Surprisingly, it is the smallest caste of workers, ones which are useless in foraging activities, that consistently approached the exit holes first and later began the morning egress from the nest. The physiological basis for the internal rhythm is unknown. The light response, however, resembles the effects of light on insect ocelli, which are generally considered to involve an increase of the general excitatory state without necessarily changing the types of motor responses (*cf.* the review of Dethier, 1953). Excitation of even a relatively small number of ants in this way undoubtedly would spread to other members of the colony, for the spread of such an increased level of activity can sometimes be directely observed. Tactile and olfactory stimulation accompanying the antennal tappings of the ants are probably involved.

The possibility of an inherent rhythm of activity operating along with a light response was recognized by Lutz (1929), although the present observations do not support several of his other hypotheses. Lutz apparently did not observe the independence of the two main types of activity outside the nest, and postulated that the amount of activity going on throughout the day might be influenced by the intensity of illumination. This possibility is not supported by the data. Once initiated by a very low intensity of light, the entire complex foraging pattern appears to operate independently of fluctuations in light intensity, until the same low level of illumination is reached in the evening. When in progress, the pattern of foraging activities seems to be determined principally by 3 factors. The first of these is the temporary indistinctness of part of the odor trail before it is strengthened by the passage of many ants. The unladen workers which proceed toward the nest at that time do not proceed the entire distance toward the nest unless they happen to be very close to it. This fact eliminates the necessity for Lutz's hypothesis that the first ants to leave the nest are "demoralized" by failure to meet any other ants and consequently return to the nest. The second change is the gradual afternoon decline in both the unladen foragers leaving the nest and the returning laden foragers. This decline probably results from the fact that foragers do not leave the nest immediately after delivering their leaves, but necessarily spend some time chewing the leaves before the smallest workers take over the job. Apparently in this colony the preparation of the substrate for the fungus gardens does not keep pace with the influx of leaves, and this eventually delays the departure of a significant number of workers. No special behavioral significance is attached to this process for in a colony with a different number of foragers, or different length trails which would also change the timing relationships, the afternoon decline in foraging activity might not occur or be large enough to be noticed. This, is fact, was the case with three smaller colonies of the same species on which brief, mostly quantitative, observations were made elsewhere on Barro Colorado. The third factor is the evening decrease in the intensity of illumination which results in another large increase of ingoing unladen ants and the failure of other workers to leave the nest. It is interesting to find that the critical intensity for stopping activity is approximately the same intensity as is effective in starting activity in the morning.

A fourth factor, which usually modifies the pattern of all activities outside the nest, consists of the heavy showers characteristic of the rain for-

est. The end result of these is a return of ants to the nest and later an egress of these ants in a manner which resembles the start of the daily foraging cycle. If the resumption of activities occurs during the late afternoon, the number of laden ants on the trail may be far greater than it would be otherwise for the time of day when the light drops below the critical intensity. This, plus delays in the return of foragers to the nest resulting from debris and weakening of the odor gradient on the trail, often leads to the appearance of prolonged nocturnal foraging activity.

The independence of the excavation and refuse-removal activity from the foraging cycle presents several physiological problems. Light evidently cannot be absolutely necessary as the only stimulus which will raise the excitatory state of the workers enough to bring about egress from the nest. It is probable that olfactory stimuli from the particles of detritus act in a similar manner. The olfactory properties of the detritus can be seen from the fact that a piece of it experimentally dropped on a foraging trail elicits a strong negative reaction from worker ants, even at a distance of several centimeters. The powerful stimulatory effects of the detritus also account for the increase in the number of workers which remove it from the nest after additional amounts accumulate during rains. The round-the-clock activity of the worker ants in detritus removal also rules out adaptation to special conditions of temperature or humidity as an explanation for intermittent foraging cycles involving the simultaneous integrated activity of large numbers of ants. In addition to the postulated necessity for light to raise the excitatory state of the workers to the point where they will simultaneously leave the nest, adaptive advantages of having a large number of ants simultaneously on the foraging trails are clear. A weak odor trail, such as results in a high proportion of disoriented ants in the morning, is thereby avoided. Removal of the debris which continually falls on the trails also requires large numbers of ants working simultaneously. Along with the effects of light, these factors provide an explanation for the existence of a periodicity of activities in the equable environmental conditions under the canopy of the rain forest.

Since there is always the possibility that results based on study of a single colony may not be typical of the species in general, an effort was made to briefly check the finding by comparison with other colonies of the species. Observations made on three other colonies of *A. cephalotes* located elsewhere on Barro Colorado Island confirmed the diurnal rhythm of foraging and the round-the-clock excavation and refuse removal. In the hope of finding exceptions to these results, colonies were sought which had their nests and foraging trails located within cleared areas, where a wider range of temperature and humidity fluctuations might bring about some modification of the typical behavior pattern. None were found, although nests and foraging trails of this species are commonly seen in second-growth forest near the edge of clearings on Barro Colorado and elsewhere in the Canal Zone, and one such nest was included among the three mentioned above. Extensive collections of this species elsewhere (Weber 1946) have shown that it is a forest-dwelling type, and the present findings are accordingly believed to be typical of the species in its normal habitat. Another possibility which has been noted by Schneirla (1947) is that during the dry season the behavior may show significant variations from the rainy-season pattern. This possibility has not been adequately investigated, since other observations on the main colony described in this report have been made only at the very onset of the dry season during 1953. Data from that period show no significant difference from those presented herein.

Summary

Through evolution of a behavior pattern which enables them to utilize an unlimited food supply, the fungus-growing ants have become established among the dominant invertebrates of the American tropics. Analysis of the behavior of *Atta cephalotes* var. *isthmicola* Weber, a typical rain-forest fungus-growing ant, reveals two types of activity cycle which operate independently. A diurnal foraging cycle is initiated by an internal physiological rhythm and light intensities of approximately 0.3 ft. candle. These factors can be experimentally demonstrated. Once begun, the pattern of foraging activities operates independently of changes in light intensity, humidity, and temperature in the normal environment, until terminated by the evening decrease in illumination. The pattern of foraging activities is modified by rain, often resulting in more noctural activity, which, however, does not prevent great differences in the amount of leaves taken into the nest from day to day. In contrast to the foraging behavior, removal of detritus from the nest proceeds continuously and there is compensation for time lost during rains by increased activity immediately afterward. Marking experiments show that the same workers may participate in foraging and detritus removal activities. The observations are consistent with the hypothesis that large numbers of workers normally leave the nest only under conditions producing an

augmented central excitatory state. The periodicity in foraging behavior which brings large numbers of ants onto the trails simultaneously is not an adaptation to special conditions of temperature or humidity. However, it appears to be of adaptive advantage in establishing and maintaining a strong odor gradient on the trail and in facilitating the removal of debris which falls or is washed onto the trails by the heavy rains which occur in this environment.

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EFFECT OF RHIZOMES OF QUACKGRASS (*AGROPYRON REPENS*) AND SHADING ON THE SEEDLING DEVELOPMENT OF WEEDY SPECIES[1]

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A number of workers have noted that substances produced by certain living plants, or produced during the decomposition of these plants, may inhibit the germination and/or the development of plants of the same or other species. Pickering (1917) concluded that certain grasses produced a leachable substance that inhibited apple trees. More recently, Proebsting and Gilmore (1940) reported that peach roots inhibited the growth of young peach trees. The development of young bromegrass plants was shown by Benedict (1941) to be inhibited by the presence of dead roots and "stolons" of bromegrass. Funke (1943) found that the plant species observed varied in their ability to tolerate a volatile substance produced by *Artemisia absinthium* L. Osvald (1947) stated that low concentrations of extracts from the rhizomes of quackgrass (*Agropyron repens* (L.) Beauv.) promoted the germination of oat and rape seed, while higher concentrations retarded and inhibited germination.

Bonner (1950) showed in studies with guayule (*Parthenium argentatum* Gray) and *Encelia farinosa* Gray that these species produced substances which affected the growth of plants. Curtis and Cottam (1950) reported that antibiotic and autotoxic effects of *Helianthus rigidus* (Cass.) Desf. appeared to be due to the presence of a substance derived from the decomposition of underground plant parts. Keever (1950) showed that *Erigeron canadensis* L. seedlings were stunted by decomposition products from *E. canadensis* roots. Brooks (1951) concluded that black walnut trees often exerted a detrimental effect on certain other plants growing within the root zone of this tree. Went, Juhren, and Juhren (1952) found that

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plant species such as *Chenopodium album* and *Amaranthus hybridus* L., varied in their ability to germinate and develop in the presence of seedling barley, tobacco, and sugar beet plants.

The present paper is based on data obtained in a supplementary study of factors which effect vegetative changes following application of herbicides to grass sods.

Methods

The study was conducted on an old alfalfa field dominated by quackgrass. The soil type of the area was a Miami silt loam of medium fertility. The study area was located on a farm of the Wisconsin Agricultural Experiment Station at Madison, Wisconsin. The following six treatments were used to observe the effects of rhizomes of quackgrass and shading on the early development of the seedlings of weedy species.

1. Rhizomes removed—artificially shaded.
2. Rhizomes removed, frozen, and replaced—artificially shaded.
3. Rhizomes removed.
4. Rhizomes not removed—clipped weekly.
5. Undisturbed check—natural shading.
6. Rhizomes removed and replaced alive—natural shading.

The study plots were 30 inches square. Four replications were used. Plates of 28-guage sheet steel, 9 by 30 inches in size, were driven six inches into the soil on the sides of each plot to prevent the encroachment of quackgrass rhizomes.

The soil was removed from the plots given Treatments 1, 2, 3, and 6 on April 22 and 23, 1953. The top inch of soil was removed, then an additional layer of five inches was removed and kept separate. Both portions of soil were sieved through a ½-inch mesh wire screen to remove quackgrass rhizomes. The lower five inches of soil were replaced immediately. On the plots given Treatments 1 and 3, the top inch of soil was then replaced and tamped so the final volume would equal that on the undisturbed areas. The rhizomes present in the plots averaged 3,000 pounds per acre oven-dry weight. On the plots given Treatment 6, the live quackgrass rhizomes removed by sieving were returned to the plots before the top inch of soil was replaced. In the plots given Treatment 2, the rhizomes removed were killed by freezing at —8° C. for 15 hours before being returned and replacing the top inch of soil. All overwintering species other than quackgrass were removed from the plots given Treatments 4 and 5.

The artificially shaded plots (Treatments 1 and 2) were covered with cheesecloth when the plots were established. The number of layers of cloth was varied so as to approximate the natural shading resulting from top growth of quackgrass on undisturbed areas (Treatment 5).

Seedlings were identified, counted, and removed every two weeks throughout the growing season.

Three physical measurements were taken to give an indication of differences in the environment near the soil surface under the various treatments. Light intensity was measured with an instrument developed by Miller (1951). This instrument was adapted to measure within a fraction of an inch of the soil surface. Two metal trays, 15 inches long, were placed in each plot as permanent guides when measuring light. Two light measurements were made each week on cloudless days between 10 and 11 a.m. and between 1 and 2 p.m. at approximately the same sun time.

Soil moisture was measured using the gypsum block method of Bouyoucos and Mick (1940). The blocks were placed at a depth of three-fourths inch to obtain data near the level of the germinating seeds and the level of the maximum concentration of quackgrass rhizomes. Soil moisture was measured often enough to give an indication of trends under different treatments.

Soil temperatures were measured by inserting several mercurial thermometers to a depth of three-fourths inch into the soil at random points in the plots. The measurements were made each week on cloudless days between noon and 2 p.m. Soil temperatures were measured at the time of day when the greatest deviation occurred between the soil temperatures of the untreated check plots and of the plots most completely denuded.

Results

The data on light, temperature, and moisture indicate little difference between the environments in the artificially shaded plots (Treatments 1 and 2), although dead quackgrass rhizomes were returned to one set of plots. Likewise, there was little difference between the environmental factors measured on the unshaded plots (Treatments 3 and 4), even though the plots given the former treatment were sieved and the quackgrass rhizomes removed. The plots given Treatments 5 and 6 showed only slight differences in light reaching the soil surface, soil temperature, and soil moisture after the reburied rhizomes on the plots given Treatment 6 had developed a top growth equal to that on the undisturbed check plots. The light and temperature trends on the naturally shaded plots (Treatments 5 and 6) were very similar to those on the artificially shaded plots (Treatments 1 and 2), but the amount of soil

TABLE I. *Seedlings removed from study plots on several dates*

Species	Number as per cent of species total								Seedlings per 150 square feet
	June		July			August		Sept.	
	3	16	1	14	28	11	24	12	
Polygonum persicaria L.	84.1	10.7	3.8	0.7	0.3	0.2	0.1	—	1,772
Polygonum convolvulus L.	81.7	13.4	3.7	—	0.6	0.6	—	—	164
Ambrosia artemisiifolia L.	74.5	13.1	10.8	1.0	0.2	0.2	—	0.2	625
Chenopodium album L.	69.0	17.3	11.7	0.3	0.6	0.3	0.6	—	323
Oxalis stricta L.	55.0	25.6	13.1	2.0	1.7	1.7	0.4	0.4	1,728
Capsella bursa-pastoris (L.) Medic.	49.4	33.6	7.9	2.5	—	5.4	1.1	—	354
Lychnis alba Mill.	42.3	15.5	19.2	5.8	4.4	8.8	3.4	0.3	1,151
Setaria lutescens (Weigel) Hubb.	39.7	30.5	19.6	4.8	2.3	2.3	0.7	0.2	4,286
Veronica peregrina L.	39.4	34.9	17.9	2.2	0.1	0.1	—	5.2	765
Trifolium repens L.	30.8	32.5	21.7	5.5	2.9	3.3	2.7	0.7	1,137
Plantago rugelii Dene.	27.3	26.8	24.9	11.5	3.3	2.8	1.7	1.6	2,656
Rumex crispus L.	32.9	16.0	7.6	9.8	4.2	22.4	6.1	1.0	407
Erigeron annuus (L.) Pers.	—	36.9	22.8	6.6	3.8	4.7	11.0	14.0	575
Amaranthus retroflexus L.	11.0	37.9	30.5	3.7	8.4	6.3	2.1	—	190
Solanum nigrum L.	25.2	31.2	34.1	5.1	0.9	2.3	1.4	0.5	349
Taraxacum officinale Weber	10.8	14.0	30.4	14.0	7.9	14.8	5.4	2.5	4,841
Other species	14.3	6.6	10.7	36.5	15.8	14.3	1.0	1.0	197
Total number	7799	4893	4368	1580	785	1248	528	319	21,520

moisture was less during drought periods on the plots with plant top growth present.

The data on seedlings removed are arranged by species and dates of removal in Table I and by species and treatments in Table II. Table III summarizes the data on seedlings of ten species comparing unshaded plots (Treatments 3 and 4) with shaded plots (Treatments 1 and 5) and plots having no rhizomes (Treatments 1 and 3) with plots having live rhizomes (Treatments 4 and 5). The total numbers of seedlings of all species arranged by treatments and dates of removal are given in Table IV.

DISCUSSION

The disturbance of the soil due to sieving did not greatly alter either the environment near the soil surface or the seedling development of weedy species. The differences in the environmental factors measured on the plots given Treatments 5 and 6 disappeared within a few weeks. The difference in the total number of seedling (Table II) on the plots given these treatments was largely due to one species, *Taraxacum officinale,* the seedlings of which were particularly numerous on the plots given Treatment 5. Minor effects were noted with *Plantago rugelii* and *Ambrosia artemisiifolia* which were favored by Treatment 5, while *Chenopodium album, Amaranthus retroflexus,* and *Solanum nigrum* were favored by Treatment 6.

If one can accept the supposition that the sieving operation did not, for most species, markedly affect seedling emergence and subsequent development, the observed differences between Treatments 3 and 4 may be explained by the response of the various species to the live quackgrass rhizomes. Except for the difference in soil moisture, the environments on the plots given Treatments 1 and 5 were very similar and the differences in seedling counts on these plots may be largely attributed to the live rhizomes present on Treatment 5. The data given in Table III show that the numbers of seedlings of *Veronica peregrina, Polygonum persicaria, Oxalis stricta, Setaria lutescens,* and *Trifolium repens* were significantly reduced and the numbers of seedlings of *T. offi-*

TABLE II. *Seedlings removed from plots given various treatments*

Species	Number as per cent of species total						Seedlings per 150 square feet
	Treatment						
	1	2	3	4	5	6	
Polygonum persicaria	69.7	6.6	21.6	0.1	1.7	0.3	1,772
Veronica peregrina	55.5	42.2	1.1	0.4	—	1.0	765
Erigeron annuus	54.8	7.3	9.7	26.0	0.2	1.9	575
Lychnis alba	47.3	9.6	9.2	18.4	7.4	7.8	1,151
Capsella bursa-pastoris	40.9	49.1	3.3	0.6	0.8	5.0	354
Oxalis stricta	39.4	28.4	7.5	4.7	9.0	10.6	1,728
Setaria lutescens	39.5	15.9	28.0	5.7	6.7	4.1	4,286
Chenopodium album	31.8	12.7	31.0	0.9	0.9	22.6	323
Solanum nigrum	25.5	32.9	18.0	10.3	0.6	12.6	349
Trifolium repens	22.7	24.1	21.3	11.6	8.8	11.0	1,137
Amaranthus retroflexus	19.4	26.8	24.2	15.2	0.5	13.7	190
Polygonum convolvulus	8.5	36.5	48.8	0.6	5.5	—	164
Rumex crispus	20.9	10.3	28.3	31.0	5.4	4.1	407
Ambrosia artemisiifolia	17.0	15.6	6.0	34.2	16.8	10.4	625
Plantago rugelii	2.2	10.9	11.6	66.5	7.3	1.3	2,656
Taraxacum officinale	5.6	2.9	5.1	30.9	36.3	19.2	4,841
Other species	35.7	23.6	9.7	23.6	2.5	4.9	197
Total number	6136	3097	3164	4543	2674	1816	21,520

cinale and *P. rugelii* were significantly greater on the plots with live quackgrass rhizomes present than on the plots with no rhizomes present. The analysis of variance for *Lychnis alba, Erigeron annuus,* and *A. artemisiifolia* indicated no significant differences between treatments, probably because of the extreme variation in the number of seedlings between the replications of a given treatment.

TABLE III. *Ratio between number of seedlings removed from plots given specified treatments*

Species	Not shaded	Shaded	No rhizomes	Live rhizomes
V. peregrina	1	37.00*	1	0.01*
P. persicaria	1	3.29*	1	0.02*
O. stricta	1	3.76*	1	0.29*
S. lutescens	1	1.37	1	0.18*
T. repens	1	0.96	1	0.46*
L. alba	1	1.98	1	0.46
E. annuus	1	1.54	1	0.41
A. artemisiifolia	1	0.84	1	2.22
T. officinale	1	1.16	1	6.24*
P. rugelii	1	0.12*	1	5.35*

*Differences exceeding the 1% LSD.

The number of seedlings of *V. peregrina, P. persicaria,* and *O. stricta* was significantly greater and the number of seedlings of *P. rugelii* was significantly less on the shaded plots than on the unshaded plots. The data on total seedlings of all species indicate that the presence of either shading or rhizomes alone was not a significant factor in the early development of seedlings, while the interaction of these factors was highly significant. The maximum number of seedlings occurred on plots that were shaded and had no live rhizomes present or those which were not shaded and had live rhizomes present. These two conditions are not usually found in nature.

The data on total seedlings in Table I indicate a progressive decrease in the number of seedlings removed during the summer. This trend was temporarily reversed in mid-summer during a period of increased rainfall. For most species the period of maximum emergence was during May. The period of maximum emergence of *T. repens, E. annuus, A. retroflexus,* and *S. nigrum* occurred during June. *Rumex crispus, L. alba,* and *T. officinale* showed increased emergence after the mid-summer rains. The number of seedlings of *V. peregrina* and *E. annuus* increased in the last count. Similar trends in the period of maximum germination of weedy species have been reported by Chepil (1946).

While the number of seedlings of some species was increased or decreased by the presence of live rhizomes, the period of maximum emergence of each species was retarded on plots wherein live rhizomes were present. Table IV indicates that the period of maximum emergence on the plots with no live rhizomes present occurred before the first count. The period of maximum emergence occurred about one month later on the plots with live rhizomes present.

TABLE IV. *Seedlings removed on several dates from plots given various treatments*

Treatment	Number as per cent of treatment total								Seedlings per 25 square feet
	June		July			August		Sept.	
	3	16	1	14	28	11	24	12	
1	52.2	27.5	14.7	2.7	0.5	0.7	0.7	0.8	6,136
2	53.7	27.7	11.4	3.6	1.6	1.0	0.4	0.4	3,097
3	50.9	26.4	13.5	3.9	0.4	2.2	1.4	0.9	3,164
4	15.6	19.1	27.7	12.9	6.7	9.3	5.3	3.3	4,543
5	12.3	13.7	29.8	15.7	7.0	14.0	5.3	2.1	2,764
6	14.9	14.1	32.8	8.4	10.2	16.2	2.0	1.2	1,816
Total number	7799	4893	4368	1580	785	1248	528	319	21,520

This phytostatic effect on weedy species in the plots having live quackgrass rhizomes present apparently is due to some influence of the live rhizomes. The plots having dead rhizomes present (Treatment 2) had an increase or a decrease in the number of seedlings of certain species, but the period of emergence of these species paralleled the period of emergence on the plots with no rhizomes present. The delay in emergence was not due to the effects of shading on the plots with live rhizomes, for the plots given Treatment 4 were clipped weekly and the period of maximum emergence was delayed as on the undisturbed check plots.

Osvald (1947) considered the responses of plants to the toxic substance present in quackgrass rhizomes to be similar to the responses of plants to plant growth substances. That is, this substance promoted the development of a given species at relatively low concentrations, while it inhibited the same species at higher concentrations. The results of the present experiment indicate that the amount of the toxic substance present under normal field conditions inhibited most weedy species, while promoting the emergence of a few species. These data appear to substantiate Osvald's findings and are interpreted as indicating that each of the species observed has a characteristic response curve to concentrations of the biologically active substance produced by quackgrass.

SUMMARY

The effects of the rhizomes of *Agropyron repens* and shading on the seedling development of

weedy species were studied in small plots located in the field.

1. Species varied in their ability to develop in different portions of the growing season.

2. The numbers of seedlings of *Veronica peregrina, Polygonum persicaria,* and *Oxalis stricta* were significantly greater and the number of *Plantago rugelii* was significantly less on the shaded plots than on the unshaded plots.

3. The numbers of seedlings of *V. peregrina, P. perisicaria, O. stricta, Setaria lutescens,* and *Trifolium repens* were significantly less and the numbers of *Taraxacum officinale* and *P. rugelii* were significantly greater on the plots with living quackgrass rhizomes present than on the plots with no rhizomes present.

4. There was usually a delay of about one month in the period of maximum emergence of weedy species on the plots having live quackgrass rhizomes present compared to their emergence on plots with no live rhizomes present.

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THE DISTRIBUTION OF INVERTEBRATES ON SUBMERGED AQUATIC PLANT SURFACES IN MUSKEE LAKE, COLORADO[1]

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Introduction

Generally speaking, the introduction of plants into a lake or pond immediately creates new niches for the existence af animal species. If the aquatic flora is increased in abundance and variety, the associated fauna is also increased in abundance and variety. Because biotic communities of this type are very complex and rather difficult to study, they have seldom been studied carefully and critically.

For some time evidence has been accumulating to show that relatively few aquatic herbivores and omnivores utilize the actual tissues of aquatic plants as food. Rather they eat the periphyton, which is the film of microorganisms, chiefly bacteria, protozoa, and algae covering submerged plant surfaces. The community structure is further complicated by the presence of macroscopic carnivores. These many species have a basic ecological relationship with the surface area of the plants. Shelford realized this when he said in 1918 that one could probably "substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations"; he at least implied that surface area as such was a very important factor, and the plant species themselves were only vehicles of the surfaces.

Krecker (1939) and Andrews and Hasler (1943) began a more detailed study of the biotic interrelationships in these communities with analyses of the abilities of various plant species to support animal populations. They found that in general the greater the leaf dissection of a submerged aquatic plant, the larger and usually the more varied was the animal population associated

[1] Contribution No. 23, Limnology Laboratory, University of Colorado, Boulder, Colorado.

with it. This is strongly suggestive of the influence of a greater surface area created by the leaf dissection.

In Lake Balaton in Hungary, Entz (1947) studied the organisms distributed over the surfaces of two species of aquatic plants. Most of the organisms he worked with were relatively small invertebrates intimately associated with the plant surfaces. He expressed his results as numbers of organisms per unit of surface area in a rather complicated system of classification of leaf and stem sizes and ecological conditions. His results very strongly indicated a considerable quantitative difference in the "coatings" of the plants with some less pronounced qualitative variations.

Important European literature on comparable marine communities was summed up by Wieser (1951). In his English summary he said, "It is held that under equal environmental conditions the number of specimens inhabiting seaweeds is directly dependent on the shape and structure of the latter, in such a way that seaweed A with a supposed specific surface 10-times bigger than that of seaweed B would also harbor an animal-population about 10-times greater than seaweed B."

Since it is very difficult to measure the actual surface area presented by a plant (Wieser used the term "specific surface"), he used an "Adsorptions-Koeffizient." This number was obtained as the weight difference between wet and dry-blotted fresh seaweeds; since the removal of the thin film of water covering the plant surface produced a loss in weight, this value was proportional to and an index of surface area. When it was "applied ecologically," Wieser found a "close relation" between "A.K." and the number of animals inhabiting a seaweed. His results actually indicated a relationship between "A.K." and abundance, but it was in no case linear as he suggested in his summary.

While these refinements in measurements in community analysis apparently yield support to Shelford's original idea concerning the influence of plant surface area, investigations on very different aspects of the ecology of these habitats are turning up other important facts. Edmonson (1940, 1944, 1946) in a series of papers on sessile rotifers discovered that many species were limited in their occurrence and distribution to the surfaces of certain aquatic plants. Later Bryden (1952) found that a species of hydra occurred on some plant surfaces and not on others. An apparent biochemical influence of some aquatic plants on the emergence of mosquito larvae was suggested by Abdel-Malek (1948). These facts are strongly suggestive of a direct influence of plants on the development of periphyton on their surfaces and even possibly on animals in the water around them. It seems reasonable to conclude that these conditions plus other unknown factors may produce a variation in the number and variety of macrometazoans which frequent the aquatic vegetation and that the relation of surface area to animal population is not nearly as simple and clear-cut as some investigations would lead us to believe.

An opportunity arose in the summer of 1950 to attempt to measure the total surface area of some rooted aquatic plants growing in Muskee Lake, Colorado. An analysis of the vegetation and its associated macrometazoans was also made in order to determine more exactly the relationships of plant surface areas to associated animal populations.

I wish to thank all those who have assisted me in this work, especially Dr. Robert W. Pennak, whose guidance and assistance were most helpful throughout the study. Grateful acknowledgment is also made to Fay Kenoyer Daily of Butler University for the identification of one of the plants, a *Chara,* and to the University of Colorado for the award of the Gardiner-Odell Summer Scholarship in Biology, which in large measure made field work possible.

Methods and Data Analysis

Muskee Lake (Fig. 1) is located in Boulder County about one mile northwest of Nederland, Colorado, at an elevation of about 8590 feet. It

Fig. 1. Muskee Lake, Colorado, looking south, May 20, 1950. Photo taken in early spring before much aquatic vegetation had appeared. Photo by R. W. Pennak.

FIG. 2. Sketches of portions of the submerged plants in Muskee Lake. A, *Chara delicatula* Ag. (X1); B, *Potamogeton gramineus* L. (X1/4); C, *Polygonum natans* Eaton (X1/4).

is small, approximately 400 feet in diameter, and shallow, measuring about three feet in depth at its deepest spot. The bottom is soft, uniform and composed of a thick layer of decaying plant material. The pond presents a uniform environment for the development of plant and animal communities.

In the summer the lake is filled with vegetation. In 1950 about 90% of the submerged vegetation consisted of four common species: *Utricularia vulgaris* L., a bladderwort; *Chara delicatula* Ag., a stonewort; *Potamogeton gramineus* L., a pondweed; and *Polygonum natans* Eaton, the water smartweed. Sketches of three of these plants are presented in Figure 2. Excluding bladderwort, it seemed quite possible that a fairly accurate measurement of surface area could be made on the other three species.

The growing season in Muskee Lake began in May and extended into November. Fourteen series of observations and collections were made every 10 to 14 days from May 20 to October 26, with the exception of two intervals of 19 and 25 days. On each collection date a number of plants of a given species were collected, the number depending on the density of the plant population. A dip net was lowered over a plant, which was gently but quickly broken off near the bottom and then lifted from the water; in the clear water the large invertebrates could be easily seen and only an occasional specimen escaped. In this manner a number of plants with their entire macrometazoan population were obtained. The associated animals were washed from the plants and preserved in the field. The plants were taken to the laboratory where they were drained, blotted on dry cotton cloth, and weighed while in this wet (damp) condition.

About midway in the season a representative collection of plants was analysed for length: wet-

weight ratios and for surface areas. Length measurements were made on *Chara* along the central axis, on *Polygonum* from the base to the tip of the leaves, and on *Potamogeton* along the stem plus the lengths of branches which contained two or more bundles of leaves. The lengths were then related to the weights of the measured plants.

The most critical part of the study was the determination of surface areas. Such measurements were made with a metric scale, dividers, and a binocular microscope. In estimating areas, the stem and leaves of *Chara* and the stem of *Polygonum* were considered essentially cylindrical; the leaves of *Polygonum* and *Potamogeton* were considered as rectangular. Appropriate formulas were applied to compute the surfaces of these structures. Since an excess area was obtained for the leaves of *Polygonum* and *Potamogeton,* a correction was made by omitting the areas of the petioles in the former and the stems and petioles in the latter. The results were as follows:

Chara—5.08 sq. cm. per 10 cm. stem length
Polygonum—23.8 sq. cm. per 10 cm. stem length
Potamogeton—281.0 sq. cm. per 10 cm. stem length

It is not implied that these are exact values; on the contrary, they are only approximations. However, with such simple growth forms as these plants exhibit, it seems reasonable to conclude that no large difference exists between the real and the computed areas.

Thus, with the above figures and the length: wet-weight ratios, each collection could be treated in terms of a given amount of surface area for each plant species. Anyone interested in obtaining more complete data on the collections should see the unpublished manuscript of Rosine (1951). This reference also includes a more complete description of the general ecology of the lake.

During the course of the study, 7,258 plant-associated invertebrates were collected, identified, and counted. Of the total, there were 5,546 amphipods (*Hyalella azteca*), 757 dipterans, 549 odonates, 162 mayfly nymphs, and less than a hundred each of beetles, caddisflies, hemipterans, mites, snails, and leeches. These groups were represented by 24 genera and an undetermined number of species. Other than the amphipod, a large majority of the animals were immature aquatic insects, most of which were not accurately identifiable to species. The genera found in Muskee Lake were typical, widespread, and common members of communities of this type.

One hundred square centimeters of plant surface area was arbitrarily selected as the unit for expressing animal population densities. In order to get some idea of the gross populations present on the three dominant aquatics, data for the seven most abundant associated animal genera were grouped (Fig. 3). Although the growing season began in mid-May, the plants were not abundant or large enough for collecting until late June. Toward the end of the season, *Potamogeton* became scarce and was not available for collection in late October. These curves show that considerable variation in density existed throughout the season. With the exception of the high density on *Polygonum* in early July, *Chara* consistently displayed the highest concentration. From the end of July until mid-October, it supported a population which was usually twice or more the size of those on either of the other two plants. Although the curves for each species show variation, the overall characteristics indicate that *Chara* had the largest number of organisms per unit of surface area; *Polygonum* was second highest; and *Potamogeton* was for the most part low.

Only one animal species was abundant enough to warrant individual treatment. Figure 4 shows the seasonal distribution of *Hyalella azteca,* the common scud. As one would expect, these curves do not depart in general from those of Figure 3, since this species comprised three-fourths of the total collection. However, the details of seasonal distribution change somewhat. *Potamogeton* supported consistently small numbers of amphipods, while *Polygonum,* in relation to *Chara,* challenged the latter's superior ability to support populations late in the season. The early-season maximum of animals associated with *Polygonum* was obviously mainly due to *Hyalella.* Amphipod populations on *Chara* gradually increased until the very end of the season, when both plant and animal populations began to decline in numbers. A pictorial representation of the distribution of *Hyallela* on August 10 is given in Figure 5. In this collection *Hyalella* showed a density distribution of about 2.0 organisms per 100 square centimeters of *Chara* surface, 1.3 per unit of *Polygonum,* and only 0.3 organisms on an equal amount of *Potamogeton.* This particular set of data was chosen because it was neither the maximum nor minimum range but represented a fairly average, mid-season pattern.

Some comments can be made concerning a few of the less abundant genera; the distribution of some forms is striking even without a detailed analysis. *Lestes,* a damselfly nymph, was represented in collections by 21 individuals; of these, only one specimen occurred on *Chara* and only one on *Polygonum. Hydaticus,* a dytiscid beetle, was never collected on *Chara* although it was found ten times among the other plants. On the

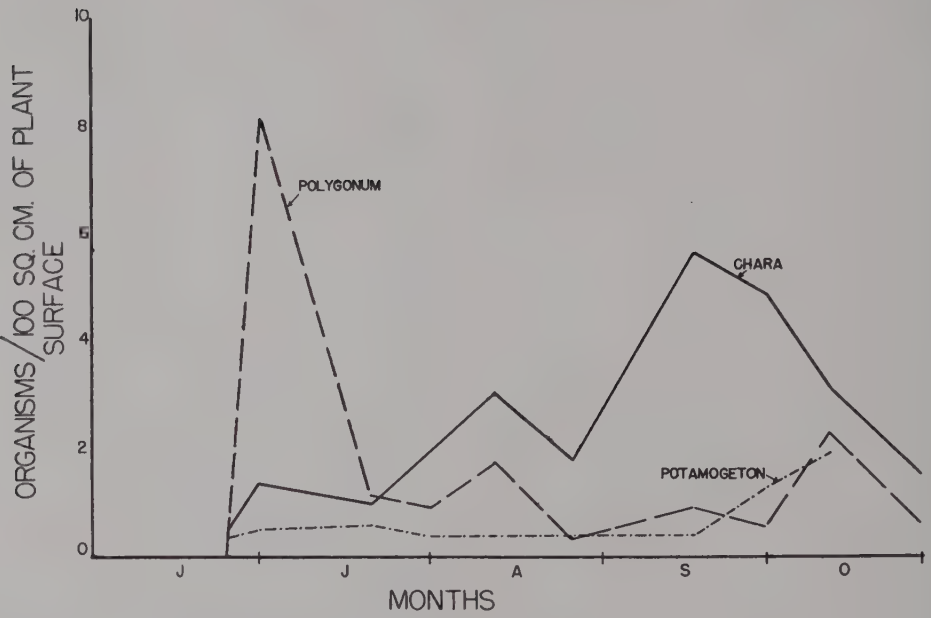

FIG. 3. Combined densities of seven genera of arthropods on three plant surfaces in Muskee Lake, 1950. Included are: *Libellula, Enallagma, Callibaetis, Phryganea, Chaoborus, Pentaneura,* and *Hyalella.*

other hand, *Laccophilus,* another dytiscid, was never found associated with *Polygonum,* whereas 24 specimens were distributed among the other plants. *Phryganea,* a caddisfly larva, occurred only twice on *Polygonum* out of a total of 57 individuals collected. Of the 64 Hydracarina collected, only one was associated with *Polygonum. Libellula,* one of the more abundant dragonfly nymphs, was never collected on *Polygonum,* although 165 individuals were scattered among the other plants. Some of the numbers are too small to warrant definite conclusions; nevertheless, further work may indicate significance for some of the restrictive distributions.

These peculiar distributions illustrate the fact that *Polygonum,* the water smartweed, supports a less varied fauna than either of the other plants studied. In general, however, nearly all of the animals collected occurred to some extent on each of the other plants. These facts recall Krecker's observation that some animal species were absent from or scarce in the vicinity of certain plant species that he studied.

DISCUSSION

Recently, Dahl (1948), as quoted by Wieser (1951), stated that the complexities of growth form in aquatic vegetation made measurement and calculation of "specific surface" areas of plants so difficult that the errors introduced invalidated the results. For the most part, Dahl was correct. Very finely dissected leaves and complicated configurations in many aquatic plants make surface determinations next to impossible. For example, the data obtained on the bladderwort (*Utricularia vulgaris*) in Muskee Lake have been eliminated from this paper because the very complicated growth form probably introduced large errors. The other three species herein treated are not particularly complicated. *Chara* and *Polygonum* are really rather simple in structure and show little variability in a homogeneous environment such as Muskee Lake. It seems quite plausible to suggest that the surface areas of these two species have been fairly accurately determined. The case for *Potamogeton* is not so positive. The scarcity of this plant made extensive collections and measurements impossible. The area determination was based on the average number of leaves (19) in a bundle (see Fig. 2); the range of variation for this species may not have been accurately determined.

But even if large errors were made in the mensuration of *Chara* and *Polygonum,* the results of the density distributions of the animals make the errors insignificant. For example, on September 18 (Fig. 4) 3.8 *Hyalella* were found on each unit of surface of *Chara* and only 0.8 per unit of *Polygonum.* In this case *Chara* supported almost five

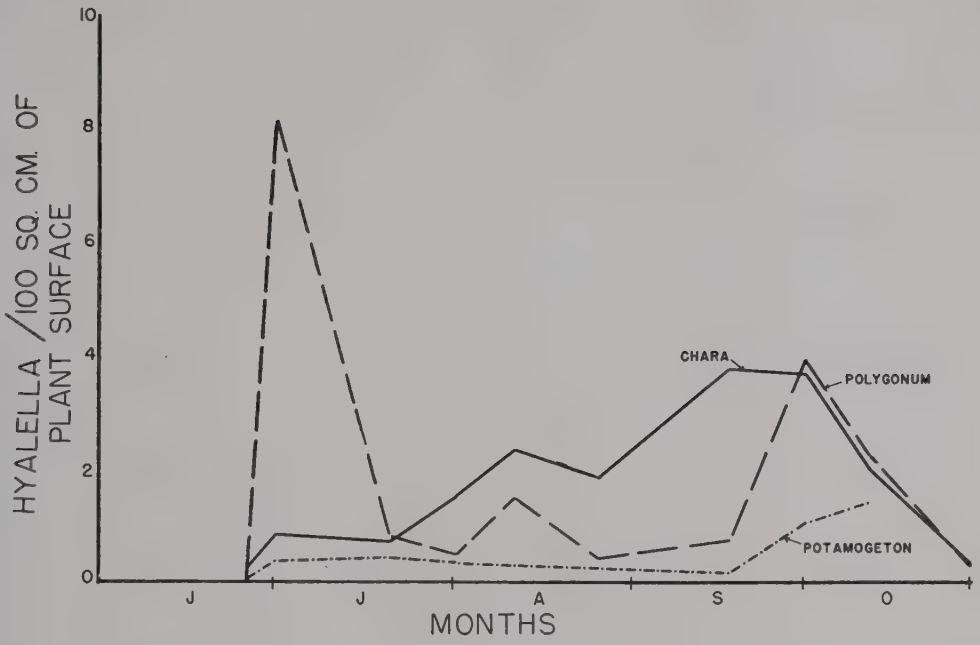

FIG. 4. Distribution of *Hyalella azteca* (Saussure) on three plant surfaces.

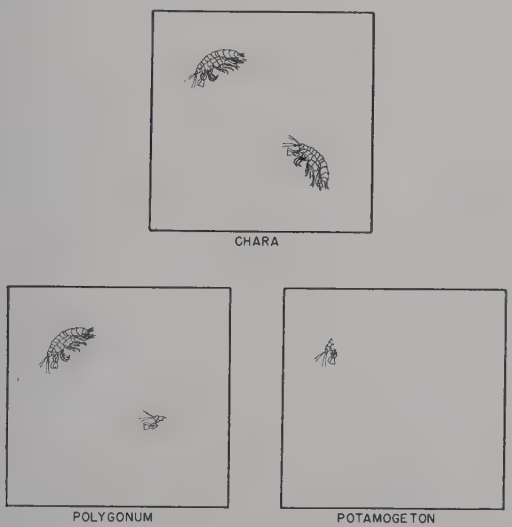

FIG. 5. Densities of *Hyalella azteca* per 100 square centimeters of surface area on three plant types, August 10, 1950. Each square represents 100 square centimeters; each figure represents one amphipod or a portion thereof in the following amounts: *Chara*, 2.0; *Polygonum*, 1.3; *Potamogeton*, 0.3.

times as many amphipods as *Polygonum*. On the three previous collecting dates *Chara* exceeded *Polygonum* by 3, 1½, and 4 times, respectively. In Figure 3 the grouped animals show a very consistent preference for *Chara* as a substratum to an even greater extent than is the case for *Hyalella* alone. Errors in the treatment of the plant material over the entire season could hardly have been of sufficient magnitude to negate such results.

Thus it is seen that animals in Muskee Lake did not utilize plant surface areas equally. Furthermore, this study shows that there were seasonal variations in the distributions of the animals over given areas of plant surfaces. Only *Potamogeton* gave evidence of a rather constant density of animals, since it supported less than 0.5 organism per 100 square centimeters of surface for fully three-fourths of the growing season. Wieser's oversimplified account of the relationships of plant surface to the associated animals is not borne out by the results of the present study. Although he worked in marine communities, problems of the sort discussed here are probably of a similar nature in all aquatic environments.

The results of the Muskee Lake collections agree with the tentative conclusions of the investigation by Entz. In his work some of the data were somewhat questionable. His observations extended over only the last five weeks of the growing season when one of the plants had already begun to decay. Windy weather and storms preceded two of his collections, and wave action apparently influenced the communities. Sampling areas were located in different environmental situations so that it was rather difficult to distinguish the causes

of differences in the fauna. Muskee Lake was subjected to none of these ecological variables. The present study indicates that plant surfaces themselves under similar environmental conditions introduce new ecological conditions which are reflected by an adjustment on the part of the fauna.

That the animals tended to show substratum preferences throughout the season is apparent from the graphs. As mentioned previously, the densities of organisms were maintained from the highest to lowest levels on *Chara, Polygonum,* and *Potamogeton,* respectively. This could appropriately be called a substratum preference for *Chara.* As would be expected, a summary of generic distributions also revealed a fauna of greater taxonomic variety on *Chara;* furthermore, *Potamogeton* harbored a more varied fauna than *Polygonum.* It should be pointed out that the low densities of organisms on *Potamogeton* should not be misinterpreted. On a plant-for-plant basis *Potamogeton* would support a larger population of animals than *Polygonum,* since there is considerably more surface area on a given weight of *Potamogeton.* In this respect, the generalization that larger animal populations accompany greater leaf dissection is true.

It would be folly to attempt to give positive reasons for the variable use of plant surface area. However, there are some facts that should be included, since they very probably are of some importance. *Chara* grows in dense beds; *Polygonum* is found in rather open patterns. Therefore equal amounts of surface area are distributed through the environment in the form of fine, interlacing plant surfaces in *Chara* and broad, continuous ones in *Polygonum.* This introduces new ecological conditions, for *Chara* offers protection and hiding places for animals as well as surface for feeding. Furthermore, leaf dissection, variations in periphyton and differing biochemical properties of plant species continue to increase the ecological possibilities. Investigations of the effects of any of these factors would certainly be worthwhile efforts in increasing our knowledge of these complicated communities.

Summary

Submerged rooted aquatic plants and their associated macroscopic invertebrates were collected in a montane pond in Boulder County, Colorado, at intervals between May 20 and October 26, 1950. These collections were studied in order to determine the numerical relationships between plant surface areas and the density and distribution of their animal populations.

The relative surface areas were measured for three common species of plants present in the lake: *Chara delicatula, Potamogeton gramineus,* and *Polygonum natans.* The density of animals was expressed as the number of macroorganisms per 100 square centimeters of plant surface area. The distribution of the seven most abundant genera over these surfaces was determined, and detailed treatment was given the scud, *Hyalella azteca,* by far the most abundant animal present in the collections.

It was found that considerable variation existed in the extent to which the animals were found on equal areas of the three plants. A typical, mid-season distribution of *Hyalella azteca* was 2.0 amphipods per 100 square centimeters of *Chara* surface, 1.3 organisms per unit of *Polygonum* and about 0.3 on an equal area of *Potamogeton.* For the greater part of the season, *Chara* harbored the largest numbers of animals per unit of area, followed by *Polygonum* and *Potamogeton,* in that order. In various parts of the season *Chara* was found to support from 1.5 to 5 times as many animals as were found on *Polygonum.* A few factors which may be involved in causing the unequal distributions of the invertebrates are mentioned.

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AN EVALUATION OF THE VARIABLE-RADIUS AND PAIRED-TREE METHODS IN THE BLACKJACK-POST OAK FOREST[1]

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Introduction

A long-term investigation on the deciduous forest frontier was inaugurated at the University of Oklahoma in 1953. Among other procedures, this program envisaged the analysis of 200 to 300 forest stands along the forest-prairie ecotone. Reconnaissance was completed in the south-central and southeastern sections of the state in the summer of 1953. During this period, 85 stands were located and described in a qualitative manner. In view of the considerable number of stands to be analyzed, it was imperative that a relatively fast method of analysis be utilized. The purpose of this paper is to compare the results derived by the variable-radius and paired-tree methods with the data obtained from the census of a blackjack-post oak forest. The writers are indebted to Prof. Joe Anderson for help in the field work and to Dr. and Mrs. John R. Whitaker for editorial assistance.

Location and Description of Stand

The stand upon which the census was executed is located 15 miles east and one mile south of Norman, Oklahoma. It is in the southwest quarter of section 25, T9N, R1E, Cleveland County. The 160 acre tract is on gently rolling topography, with a ravine traversing the western portion in a north-south direction. According to reliable information, the tract had never been cut over, had been grazed only lightly, but had been burned-over periodically. The stand is fairly dense with considerable woody undergrowth on the slopes and in the flats along the ravine, but is rather open with a good grass cover in the higher and drier portions of the tract.

The dominants, as indicated both in the reconnaissance and in the census, are blackjack (oak), *Quercus marilandica* Muenchh., and post oak, *Quercus stellata* Wang. Common secondary species are (black) hickory, *Carya texana* Buckl., and black oak, *Quercus velutina* Lam. Twenty-three other woody plants, as well as numerous grasses and forbs, were encountered in the stand but are omitted from consideration in this discussion. Except for the summary, only common names will be used in the present paper.

[1] Contribution of the Oklahoma Biological Survey, Dr. Carl D. Riggs, Director.

Results of Census

In preparation for the census of the blackjack-post oak stand, two rectangular plots of slightly different composition were delineated by painting rings on the boundary trees. These units, designated as south and north plots, possessed areas of 4.36 and 4.63 acres, respectively. In sampling, all woody plants with a DBH of three inches or more were measured and entered on a form. From these data, the following compilations were made for each tree species in the south plot, in the north plot, and in the entire stand: number of trees, trees per acre, relative density, total basal area, and basal area per species.

It will be observed that the composition of the south and north plots varied somewhat although the order of abundance was similar (Table I). In the south plot, there were considerably more blackjacks than in the north plot, whereas there were fewer post oaks, hickories, and black oaks. The number of trees per acre was greater in the south plot.

Compared with most deciduous forests, the total basal area is very low (52.3 square feet) in the blackjack-post oak stand. Of the basal area for the entire stand, blackjack and post oak contributed over 86 per cent. Although blackjack trees outnumbered post oak trees by more than two to one, the basal areas of these species were similar in both plots (Table I). This is correlated with the fact that only one per cent of the blackjacks, as against 28 per cent of the post oaks, possessed a DBH of 12 inches or over. Compared with the post oak, the blackjack had the higher basal area in the south plot but a lower value in the north plot. This reversal is due primarily to the lower number of blackjack trees in the north plot (Table I).

Description of Variable-Radius and Paired-Tree Methods

The variable-radius method of forest sampling was developed in Germany by Bitterlich and introduced into the United States by Grosenbaugh (1952a, 1952b). More recently this method has been compared with the paired-tree technique of Cottam and Curtis (1949) in Appalachian forest types by Shanks (1954). The variable-radius method is based on the principle of point sam-

TABLE I. *Number of trees and basal area in the blackjack-post oak forest according to the complete census*

Species	South Plot			North Plot			Entire Stand		
	Trees	No./acre*	Basal Area Sq. ft./acre	Trees	No./acre*	Basal Area Sq. ft./acre	Trees	No./acre	Basal Area Sq. ft./acre
Blackjack	593	136.0	25.3	395	85.3	21.3	988	109.9	23.3
Post oak	204	46.8	20.3	231	49.9	23.6	435	48.4	22.0
Hickory	83	19.0	4.2	125	27.0	7.1	208	23.1	5.6
Black oak	21	4.8	0.9	37	8.0	2.0	58	6.4	1.4
Totals	901	206.6	50.7	788	170.2	54.0	1689	187.8	52.3

*South plot, 4.36; North plot, 4.63 acres.

pling. A hand-held angle-gauge is used to determine those trees which are within a distance from the sampling point no greater than 33 times their diameter. The angle-gauge is made by mounting a crossarm, one inch wide, at one end of a 33-inch stick and a similar piece of metal or wood, with a peephole near its center, at the other end. With this angle-gauge, the angle has been so selected that the tally at a given point need only be multiplied by a factor of 10 to yield basal area in square feet per acre. Thus, a tally of 7 trees at a point would indicate a basal area of 70 square feet per acre and if this tally were composed of 4 blackjacks and 3 post oaks, then basal areas per acre of 40 square feet and 30 square feet respectively would be indicated.

The paired-tree method also is based on the principle of point sampling. At a given point, the pair of trees is selected as follows: "the first is the tree nearest the sample point, the second is the tree nearest to the first outside the 160° sector bisected by a line from the sample point to the first tree. Diameters of the sample trees and distances between them provide the basis for computing stand composition" (Shanks 1954). The standard practice in Wisconsin has been to use trees 4 inches or more in diameter and to use 40 points, or 80 trees, per stand. In the present study, a lower limit of 3 in. DBH was selected because of the small size of all trees in the blackjack-post oak forest. Forty points were utilized in both the variable-radius and paired-tree techniques.

Choice of a Method

In deciding on a method for analyzing the 200 to 300 forest stands along the deciduous forest frontier, three considerations were paramount: 1. the method must be rapid, 2. it should require little equipment, and 3. it must include data for frequency, density, and basal area compilations. Both the variable-radius and paired-tree methods met the first two requirements readily. Regarding the third item above, Shanks (1954) stated that, "variable-radius plotless sampling is an efficient means of assembling forest stand data, in terms of square feet basal area per acre and percentage composition and their variability. . . . Frequency data are directly available, but they differ from the usual frequency data. . . . they express the frequency of effective vegetational contribution rather than frequency of botanical presence." Curtis and Cottam (1949) declared that the random pairs method, "proved to be a very rapid and reasonably accurate means of obtaining the frequency, density and dominance [basal area] of the tree species of oak opening, oak-hickory, and maple-basswood forests." Unfortunately, the variable-radius method proved unsuitable for determining frequency and density and the paired-tree method did not provide sufficiently accurate data on frequency, density, or basal area. We have resorted, therefore, to a combination of the variable-radius method for basal area data, and arm-length transects between sampling points for data on frequency and density.

Defects of the Variable-Radius Method

The variable-radius method has been used by Shanks (1954) for determining frequency. It has been used also for the construction of phytographs which include density and frequency data (Shanks 1954). In the study of the blackjack-post oak forest, the data on relative frequency by variable-radius sampling did not agree closely with those derived from transects. According to the variable-radius technique, the frequency was too low for blackjack and too high for post oak (Table II). Since the blackjacks were somewhat smaller than the post oaks, it was thought that the larger trees might have been favored by the variable-radius method.

To test this theory, a theoretical population was fashioned as follows: a grid of heavy lines one inch apart was constructed and another series of light lines one-third of an inch apart was placed between the original lines, thus giving a grid of one-third inch squares. Then symbols represent-

TABLE II. *A comparison of data in the blackjack-post oak forest obtained by the complete census, arm-transect, paired-tree, and variable-radius methods*

Species	Number per Acre			Relative Density			Relative Frequency		
	Census	Transect	P–T	Census	Transect	P–T	Transect	P–T	V–R
Blackjack	109.9	130	68.7	58.5	60.5	44.9	53.8	42.7	38.8
Post oak	48.4	45	38.6	25.8	20.9	25.2	23.1	25.0	34.7
Hickory	23.1	25	40.2	12.3	11.6	26.2	15.4	27.9	19.4
Black oak	6.4	15	5.7	3.4	7.0	3.7	7.7	4.4	7.1
Totals	187.8	215	153.2	100	100	100	100	100	100

ing large trees were placed at the intersections of the heavy lines and other symbols depicting small trees were established at the junctions of the light lines. This provided a theoretical, hypodispersed population of trees, with small trees eight times as numerous as the large trees. Since the small trees were assigned a diameter one-third that of the large trees, the small trees on the grid would be sampled at a maximum distance of one-third that of the large trees by the variable-radius method. It was a simple matter to establish sampling points and to tally the population with the aid of a strip of cardboard with crossmarks one-third of an inch and one inch from the end held at the sampling point by a pin. With a sample of 30 points, the frequency percentage for both small and large trees was 100. The maximum plot radii for sampling the theoretical population by the variable-radius technique were changed, therefore, to 1/12 inch and 1/4 inch for the small and large trees respectively. When the population was sampled under the above conditions, trees of each diameter were recorded at 9 out of a total of 30 sampling points, giving a frequency percentage of 30 for each tree size. Since the small trees were eight times as numerous as the large trees a much higher frequency percentage (80-100) for the small trees might have been expected. This exercise demonstrates that meaningful frequency values cannot be determined by the variable-radius method in a population with different tree diameters. Apparently Shanks (1954) also realized that frequency was affected by tree size since he stated that, "only those minor species which are consistently of small size tend to have values lower than their conventional plot frequency values in the stand, such as serviceberry, mountain holly, and mountain ash in Table I."

Densities can be computed from basal area data obtained by the variable-radius method if size distributions are known. This, of course, necessitates estimating or measuring the diameter of each tree and tallying it in its appropriate diameter class (Shanks 1954, Grosenbaugh 1952a). This procedure demands more time in the field and also requires considerable extra time for calculations. Moreover, the variable-radius method is not suitable for the determination of sapling density because of the relatively small diameter of saplings.

Defects of the Paired-Tree Technique

A comparison of the data on density derived from the paired-tree technique with those from the complete tree census is presented in Table II. On the basis of data procured by this technique, the number of blackjack trees was much too low, the count of hickory trees was too high, and the total tally of all trees was too low when compared to the numbers derived from the census (Table II). Furthermore, the order of abundance with reference to post oak and hickory was reversed by the paired-tree method. On the basis of relative density (percentage of total trees), the same relation obtains: blackjack too low and hickory much too high (Table II). Since no frequency data were taken in the census, the relative frequencies by the paired-tree method will be compared with those derived from 40 arm-length transects of 0.01 acre each. It will be observed that the relative frequencies, by the paired-tree technique, are too low for blackjack and too high for hickory (Table II), a relationship very similar to that obtained for density and relative density.

In the matter of basal area, the paired-tree technique was also quite inaccurate. Basal area of the blackjack, as well as the total basal area, was much too low. Furthermore, the order of blackjack and post oak, with reference to basal area, was reversed by the paired-tree method (Table III). It is possible that an improvement might be made in the paired-tree method if a new exclusion angle were determined, but this was not attempted.

An advantage of the paired-tree technique was the relatively small time of sampling (2.5 hours for 40 points). However, considerable time was required in making compilations. For the variable-radius method, approximately two hours were required for a 40-point sample. Since this method

TABLE III. *A comparison of basal area data in square feet per acre in the blackjack-post oak forest determined by the complete census, variable-radius (three samples), and paired-tree techniques*

	Census	Variable-radius			Paired-tree
		First	Second	Third	
Blackjack...	23.3	28.0	24.5	24.0	16.4
Post oak....	22.0	20.8	22.2	19.5	19.9
Hickory....	5.6	7.2	4.0	3.8	4.6
Black oak...	1.4	2.0	2.8	1.8	1.6
Totals.....	52.3	58.0	53.5	49.1	42.5
Percentage Deviations..	Base	+10.9	+ 2.3	− 6.1	−18.7

was not deemed desirable for obtaining density and frequency data in the blackjack-post oak forest an additional hour was required for 40 arm-length transects of 0.01 acre each. It is probable, therefore, that there is little time differential between the paired-tree technique and the augmented variable-radius method. The latter method, however, was selected because of its greater accuracy.

The Augmented Variable-Radius Method

In the first sample by the variable-radius method, the basal area for the blackjack oak and the total basal area were somewhat higher than comparable data derived from the complete tree census (Table III). It was decided that this discrepancy might be due to the fact that the angle-gauge had not been calibrated. The angle-gauge must be fitted to each investigator, depending on the depth of the eyes and whether the worker wears glasses. This calibration was made according to the instructions given by Grosenbaugh (1952b): "The cross-piece, when viewed through the peep-hole, should exactly cover a 3-foot horizontal intercept at a distance of 99 feet from the eye. The distance between the cross-piece and peep-hole should be adjusted till this occurs." Using the calibrated angle-gauge, the basal area data were very similar to those procured by the census (Table III, second and third samples). Whereas the percentage deviation from the total basal area was + 10.9 in the first sample, those of the second and third samples were + 2.3 and − 6.1 respectively. In view of the fact that a deviation of ± 10 per cent is to be expected in any method of forest analysis, these data are excellent indeed.

Mean basal areas (sq. ft./acre) in the first sample by the variable-radius technique, with accompanying standard errors, were as follows: blackjack, 28.0 ± 2.5; post oak, 20.8 ± 2.5; hickory, 7.2 ± 1.6; black oak, 2.0 ± 0.7; and total, 58.0 ± 3.3. In the case of the dominants, blackjack and post oak, the standard errors approximated 10 per cent of the means. For the total basal area the standard error was much less (5.5%) than 10 per cent of the mean. Although the above data are not as reliable as those procured by Shanks (1954), it is believed that the sample utilized (40 points) is adequate for the determination of basal area in the blackjack-post oak forest.

In connection with the reliability of data on relative density, Cottam, Curtis and Hale (1953) state that, "Reasonable accuracy was attained when the number of individuals of the species in question exceeded 30 in the total sample." It will be observed that average tallies of 102 and 83 trees, respectively, were recorded for the dominant trees by the variable-radius technique (Table IV). These tallies are about three times the 30-tree figure suggested in the above statement. Significant also is the fact that the average total sample (216) was more than the number of trees per acre (188) according to the complete tree census. These findings also lend support to the belief that the sample of 40 points, by the variable-radius method, is adequate for forest analysis along the forest-prairie ecotone.

Since the variable-radius method proved undesirable for determining density or frequency, recourse was had to a series of paced, arm-length transects of 0.01 acre each between the 40 sampling points. It should be pointed out that the length of one's pace varies with such items as slope and obstructions, and that the total area covered would only approximate 0.40 acre. Although the absolute number of trees per acre might be changed, the relative number of trees (relative density) would not be affected. In the one sample presented, the number of trees per acre by the arm-transect method approached the census numbers fairly closely (Table II). Relative densities by this method also approximated the census figures. Since no frequency data were taken in the census, there are no frequencies with which the relative frequencies obtained by the arm-transect technique can be compared. How-

TABLE IV. *Number of trees, tallied in three samples by the variable-radius method*

	First	Second	Third	Average
Blackjack...	112	98	96	102
Post oak....	83	89	78	83
Hickory.....	29	16	25	23
Black oak...	8	10	7	8
Totals....	232	213	206	216

ever, it will be noted that the relative densities and relative frequencies obtained by the arm-transect technique are very similar (Table II).

Spatial Distribution of Individuals

Cottam, *et al.* (1953) stated that . . . "The student of plant communities is concerned with the distribution of objects in space. His first problem is the determination of the kinds of plants present and their relative numbers. Since it is usually impossible to examine all of the plants present, he confines himself to some kind of a sample of the vegetation . . . the results [of sampling] are affected in their accuracy by the actual dispersion of the plants on the ground. . . . Many of the methods now in use presuppose a random distribution of individuals in the population and are satisfactorily accurate when such conditions prevail." Goodall (1952) pointed out that if a species is randomly dispersed, density is the only additional information necessary to give a full description of its distribution. Based on samples from an artificial population, Curtis and McIntosh (1950) found that frequency values are too low for any given density if the species has a contagious distribution and too high if the species is hypodispersed. These same workers reported that density determinations are relatively similar for all three types of dispersion, but that there is some indication that highly contagious species are over-represented by relatively small quadrats.

The variable-radius sampling method furnishes data in such a form that the spatial distribution of the individuals of any given species can be rapidly calculated. Using data obtained by the variable-radius method, the distribution of the individuals of each of the four common trees of the blackjack-post oak forest was determined first by calculating the coefficient of dispersion, $K = \frac{V}{\bar{x}}$. In the above formula V equals the variance and $\bar{x}$ equals the mean number of individuals at each point. Using the limits for random distribution of $K = 1 \pm 2\sqrt{\frac{2n}{(n-1)^2}}$ (where n equals the number of sampling points), set by Blackman (1942), the individuals of all four species were indicated to have a random distribution (Table V).

The chi-square test for the fitted Poisson distribution was next applied to each species since the coefficient of dispersion, as pointed out by Blackman (1942), "is not a sensitive test for certain skew distributions." Again, a random distribution was indicated for all four species.

Since the chi-square test for the fitted Poisson distribution is a much more reliable indication of a random distribution, it is strongly recommended

Table V. *Spatial distribution of tree species in the blackjack-post oak forest*

	K-value*
Blackjack	0.90
Post oak	1.22
Hickory	1.42
Black oak	1.08

*$K = \frac{V}{\bar{x}}$. Random distribution indicated if $K = 1 \pm 0.46$ using limits set by Blackman (1942).

that such a procedure be followed. Poisson series based on means from 0.001 to 100 can be quickly set up by reference to Table I of Molina (1943). By use of that table, the above tests can be completed more rapidly than the coefficients of dispersion can be calculated. The test for blackjack is given as an example of the procedure in Table VI. It will be noted that the chi-square is quite small indicating a very close fit between the sample data and the appropriate Poisson series.

Table VI. *Comparison of distribution of individuals of blackjack with the appropriate Poisson series*

Number of individuals	Number points	Expected number for Poisson dist.	Deviation	Dev.²/Expected
0	2	2.4	9.2	1.2	0.16
1	6	6.8			
2	11	9.5	1.5	0.24
3	9	8.9	.1	0.001
4	6	6.2	.2	0.006
5	4	3.5	6.0	0	0.000
6	1	1.6			
7	1	0.7			
8	0	0.2			

m=2.8 n=40 Chi-square=0.407*
Degrees of freedom=3

*A random distribution is indicated since the sample does not depart significantly from the Poisson series.

Summary

1. An evaluation of the variable-radius and paired-tree plotless sampling methods is presented herewith.
2. The standard for comparison was a complete tree census of a blackjack-post oak forest with blackjack, *Quercus marilandica* Muenchh., and post oak, *Quercus stellata* Wang., as the dominant trees, and hickory, *Carya texana* Buckl., and black oak, *Quercus velutina* Lam., as common secondary species.
3. In the stand investigated, the blackjacks were twice as abundant as the post oaks but had about the same total basal area.
4. The variable-radius method was found to be

unsuitable for obtaining data on frequency since large trees were favored by the sampling gauge. This method proved to be undesirable, also, for determining density for the following reasons: (1) extra time is required in the field to estimate the diameter class of each tree sampled, (2) considerable time is required for calculations and (3) the method is unsuitable for determining the density of saplings. The method proved very satisfactory for procuring data on basal area.

5. The paired-tree technique proved to be useful for procuring data on density, frequency, and basal area but was insufficiently accurate, due probably to the small sample utilized.
6. An augmented variable-radius method was chosen for future forest analysis. This consisted of the usual variable-radius technique for determining basal area, supplemented by 40 arm-length transects of 0.01 acre each for procuring data on density and frequency.
7. The variable-radius sampling method furnishes data in such a form that the spatial distribution of the individuals of any given species in a stand can be determined readily. Knowledge of the type of dispersion is important in interpreting any other kinds of information obtained about the stand. All four common tree species sampled by the variable-radius method in the blackjack-post oak forest were found to be randomly dispersed.

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ACTIVITY PATTERNS OF PERCH, *PERCA FLAVESCENS*, IN RONDEAU BAY OF LAKE ERIE[1]

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Introduction

The data for this investigation to determine the daily periods of the activity of perch were obtained by the use of gill-nets set in Rondeau Bay during the summers of 1951 and 1952. Rondeau Bay, with a maximum depth of 10 to 12 feet, is about five miles long and two miles wide (Fig. 1). It lies in Ontario on the north shore of Lake Erie, opposite Cleveland. It was connected to the lake only by a channel about 100 yards wide until the spring of 1952. At that time storms broke through the sand bar between the lake and the bay at site H. A second gap was formed just east of the former gap in the autumn of 1952.

Weekly net settings in 1951 revealed that different species of fish could be caught more readily at certain times of day than at others. In 1952, the investigation was directed towards the study of perch, *Perca flavescens* (Mitchill), because this species made up 90 per cent of the catch and showed a marked pattern of activity.

The capture of fish in gill-nets is an index of the activity of fish present in the area since the more active a fish the greater its chance of encountering the net and the less its chance of avoiding it. Also, the number of fish caught depends upon both the abundance of fish in the vicinity of the nets and the activity of the individual fish. Other factors, such as the amount of light, the turbidity and the manner in which the net is set, may influence the fish's chance of avoiding the net. If the fish move to another area for a portion of the day, then the net catches would reveal only the activity in a particular locality and would not give a true picture of activity. Thus, the rate at which non-migratory fish are caught re-

[1] This paper is based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Zoology at the University of Western Ontario, London, Ontario. Author's present address: Central Fisheries Research Station, Winnepeg, Manitoba.

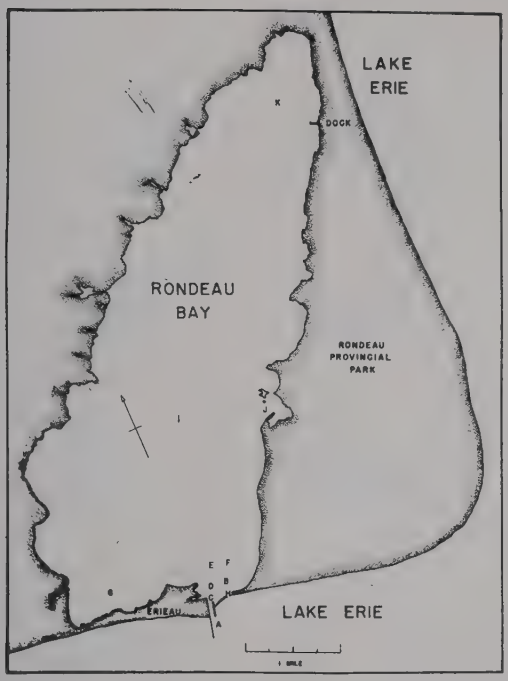

FIG. 1. Rondeau Bay showing sites of net settings.

veals the amount of their activity during the whole day, but the rate of capture of fish which migrate daily reveals only the amount of activity during part of the day.

Recently there has been an increasing awareness that many animals are adjusted to their environment so that they can carry out their activities better at certain times of day than at others. The reviews of literature on the subject by Calhoun (1945) and Welsh (1938) show that a considerable portion of the studies has been done on specialized subjects such as oxygen consumption, body temperatures, and movements of eye and body pigments. Most of the work on general activity involves insects and mammals.

Workers who have dealt with non-migratory perch agree that they are active during the whole period from dawn to sunset and are inactive at night. Pearse and Achtenberg (1920), working in Lake Mendota, Wisconsin, found that the perch had only a slight upward migration at night. Three days of four-hourly liftings of a net just above the thermocline showed that the activity built up from a low at 0100-0300 hours to a peak at 1600-2000 hours and then decreased. Carlander and Cleary (1949), found that in Lake of the Woods, Minnesota, and in Clear Lake, Iowa, perch were more active during the daytime and that in shallow water more were caught in the afternoon than in the morning. Sieh and Parsons (1950) found that perch of Clear Lake, Iowa, were more active in daylight hours, and in shallow water up to five feet deep more perch were caught in the latter half of the daylight period.

In dealing with migratory perch of Lake Mendota, Wisconsin, Hasler and Bardach (1949), found that at 40 to 60 minutes before sunset perch appeared in schools of 50 to 200 fish. At two sites perch approached the shoals, then turned at the 16-foot contour and swam parallel to the shoal. The perch feed on swarms of *Daphnia* which were gathered there by currents. The perch arrived earlier as the sun set earlier. Their arrival as detected by gill-nets, electric eyes, and diving corresponded to an increase in the catch by anglers. These migrations started gradually near the end of May and ended gradually in mid-October. At two other sites in the lake no migration was detected.

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METHODS

All fish used in this study were caught by gill-nets set at the sites indicated on the map (Fig. 1). The nets used in 1951 were 1½-, 1¾-, 2⅛-, 2¼-, 2¾-, and 3½-inch mesh (stretched measure) cotton gill-nets, 165 feet long and 50 meshes deep except for the 3½-inch mesh nets which were 36 meshes deep. A 50-foot net, made by sewing ¾-inch milliner's veiling to a gill-net, was also used on one occasion. During 1952, nylon mesh nets were used in every case except at site C on July 1-3 when a 1½-inch cotton net was used and at site B on August 27-28 when the net made of milliner's veiling was set. It was expected that the change to nylon mesh would give a truer measurement of the activity pattern since the nylon is seen less readily and would be avoided less during the daylight hours. Principally 1½-inch nets were used in order to catch two- and three-year-

old perch but other sizes including 1¾-, 2-, 2¼-, 2½-, and 3-inch mesh were used in an attempt to catch older perch and other species of fish.

Beginning on July 19, 1951, the fish were removed from the nets at four-hourly intervals at 0300, 0700 hours,[2] etc. Each time that the nets were set from August 3 to September 10 they were cleared at 0500 and 1700 hours in addition to the four-hourly liftings. The first two net settings in 1952 were made in the above manner. In the remaining settings the nets were lifted at one hour before sunrise, to remove the fish caught overnight, and then hourly until the sunset peak was finished. The nets were lifted at noon and then hourly from four hours before sunset until one or two hours after sunset. If the nets had been lifted more frequently than at hourly intervals, a large proportion of the fish would have been missed.

To compare the rates at which fish were caught, the number of fish in each lifting was converted into the number per hour per net for each species. To add together the number of fish per hour for several net settings, it was assumed that the fish were caught at an even rate in the period between any two liftings. Thus, if the nets were cleared at 0715, 0815, and 0930 hours and if the number of individuals of a species removed at 0815 was twenty and the number at 0930 was ten, then the number caught between 0800 and 0900 hours was eleven. By calculation five were caught between 0800 and 0815 hours and six between 0815 and 0900 hours.

The various graphs in Figure 2 were obtained by converting the number of perch caught at each net lifting into the rate of capture in hourly or quarter-hourly intervals. The splitting of intervals between net liftings spreads the peaks and troughs over longer time periods and thereby makes them less distinct. The times of both the liftings and peaks changed progressively during the season with the change in time of sunrise and sunset as shown in Figure 4. The averaging of the peaks for the whole summer caused additional leveling of the peaks. Some intervals between liftings covered several hours and occasionally this interval covered a period of low catches and part of a peak. The majority of the perch were presumably caught in a small portion of the time interval so that in such cases the average rate does not give a true picture of the situation. Thus the activity pattern for a single day was much more distinct than the averages show, especially when

[2] All times mentioned are Eastern Standard Time. Local solar time was 5.463 hours later than Greenwich Mean Time.

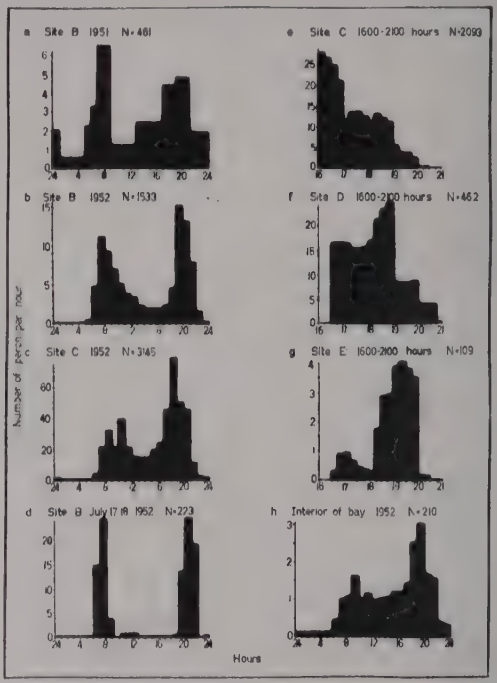
a Site B 1951 N=481
b Site B 1952 N=1533
c Site C 1952 N=3145
d Site B July 17 to 18 1952 N=223
e Site C 1600-2100 hours N=2093
f Site D 1600-2100 hours N=462
g Site E 1600-2100 hours N=109
h Interior of bay 1952 N=210
Number of perch per hour
Hours

FIG. 2. Activity patterns of perch as measured by the rate of capture in gill-nets for hourly intervals. The number of fish used in each graph is indicated by *N*.

the peaks matched the intervals between liftings. An example of a nearly ideal activity pattern is shown in Figure 2d.

In 1952, the direction in which the perch were headed when caught in the net was recorded. Occasionally when a perch was badly tangled in a net or when mangled by a predator, it was impossible or impractical to determine its direction of movement. Also, when catches were large only sample directional counts were made at each lifting in order to return the nets to the water as soon as possible.

In 1952, the perch stomachs were preserved in 10 per cent formalin for later microscopic examination. A maximum of 25 stomachs from a net lifting was analysed. The volume of the stomach contents was found by placing three millilitres of the preserving fluid in a 10-ml. graduated cylinder and recording the increase in volume when the stomach contents were added. For the occasional large food item a 50-ml. graduated cylinder was used. The volume of each of 21 categories of food items was measured, or if less than 0.05 ml., it was estimated by sight.

Activity Pattern

The activity pattern of perch, mostly two- and three-year-old fish averaging 13.45 cm. in length, at various sites is presented in Figure 2a-d. The 461 perch caught at site B (Fig. 1) in two- and four-hourly liftings during 1951 are shown in Figure 2a. Perch caught at the same site in 1952 are shown in Figure 2b: (the nets were lifted hourly during the peaks and less frequently at other times). The peaks, referred to as sunrise and presunset peaks, occurred at essentially the same hours in both years. The slight difference in the time of the peaks is due to the different intervals at which the nets were lifted, as well as to the difference in the months during which the nets were set. The difference in the magnitude of the peaks, in terms of the number of perch per hour, was probably due to the change from 1¾-inch cotton mesh nets to 1½-inch nylon mesh nets.

Figure 2c shows the activity pattern at site C, located in the channel between the lake and the bay. Essentially the same type of activity pattern was shown as at site B except that the rate of capture of perch was much greater at site C. The sunrise peak occurred earlier at site B than at site C and the presunset peak was earlier at site C than at site B. This suggested a daily migration from site B to site C during the sunrise peak and a return during the presunset peak. Later in the season a net set at site A indicated that the perch migration extended into Lake Erie.

The activity pattern of perch caught at sites G, I, J, and K combined is presented in Figure 2h. The perch at these sites in the interior of the bay had only a slight sunrise peak and showed relatively more activity at midday than did the perch at sites nearer to the lake, e.g. sites B and C.

Nets were set at sites C, D, and E which were less than one-sixth of a mile apart in a straight line running from the channel into the bay. The rate of capture of perch during the presunset peak at these sites in 1952 is shown in Figure 2e-g. These graphs show a chronological successsion of peaks from site C to site E. This suggested that during the presunset peak there was a migration of perch from site C to site E which in turn suggested that the perch were migrating from the lake into the bay during this period. The marked decrease in abundance from site C to site E (note the change in scale) suggested that the perch spread out as they entered the bay. The small catches at sites E and F (the latter not shown in Fig. 2), together with the time lag in the peaks between sites C and E, indicated that the perch did not go much beyond the former sites. During a few diving operations near sites D and E, perch were observed feeding in small schools. They appeared to swim back and forth as they fed but gradually moved from site C toward site E. The considerable lapse of time between the peaks at successive sites also supports this idea.

Very little information was obtained on the young-of-the-year and yearling perch. A net made from milliner's veiling set at site B on August 2-3, 1951, caught 34 young-of-the-year perch. They were inactive at night but there were insufficient data to determine the type of their activity during the daytime. A repetition of the net setting in 1952 caught only minnows but the presence of young perch in the stomachs of older perch and of other species of fish indicated their occurrence in the bay.

The setting of larger mesh nets in the bay failed to catch perch 25 cm. long or longer, and as they were not caught by anglers, it can be safely assumed that the large perch did not occur in the bay in the summer. Some nets set in the marsh at the southwest corner of Rondeau Provincial Park (Fig. 1) caught a few large perch, one of which was seven years old. However, these were a very dark colour, which together with the fact that none was caught in the bay, indicated that they remained within the marsh.

Directional Counts

In the interior of the bay, at sites G, I, J and K, approximately equal numbers of perch were headed in each direction when caught in the nets. Since there was no tendency for the perch to head in a particular direction at any time of day it was assumed that no regular migration took place in the interior of the bay.

At site C the nets were set at right angles to the channel connecting the bay and the lake. The directional counts presented in Table I showed a significantly larger number of perch headed toward the lake during the sunrise peak and a significantly larger number headed towards the bay during the presunset peak. At other times of day there was no significant difference in the number headed in either direction as indicated by the Chi-square test.

The net setting at site A, which was set during a presunset peak only, showed a significantly larger number headed toward the bay. The directional counts during a single day at site H showed a presunset migration into the bay and a larger number headed toward the lake in the sunrise peak but the numbers were too small for a significant difference. The net settings at sites D, E and F also showed more perch headed toward the lake during the sunrise peak and more

TABLE I . *Directional counts of perch at site C. In each column the number on the left indicates the number of perch headed into the bay and the number on the right the number headed into the lake.*

Date	Midnight to sunrise peak	Sunrise peak	Sunrise peak to noon	Noon to presunset peak	Pre-sunset peak	Presunset peak to midnight
July 1-3.....	9 – 8	88 – 87	0 – 0	7 – 32	54 – 35	5 – 6
July 9-10.....	0 – 1	71 – 108	40 – 56	75 – 55	117 – 90	5 – 2
July 17-18.....	1 – 4	9 – 34	1 – 4	0 – 0	34 – 62	2 – 6
July 25.....	.....	.....	.....	.....	237 – 104	.....
July 30.....	.....	.....	.....	.....	106 – 33	.....
Aug. 28-29.....	.....	.....	.....	.....	57 – 12	.....
Total.....	10 – 13	168 – 227	41 – 60	82 – 87	605 – 340	12 – 13

headed toward the bay during the presunset peaks than in the opposite directions. However at site B there was a slight contradiction in that there was a significantly larger number of perch headed toward the lake at both peaks. Unfortunately for the purpose of directional counts, the nets were set at only a slight angle to the path of the migration (see below). Thus a slight difference in the path of the sunrise migration could cause the perch to enter the net from the opposite direction.

The directional counts indicate that the perch migrated daily from the bay to the lake and back. The most probable route for the presunset migration is presented in Figure 3. The perch, returning from the lake, passed site A, passed through the channel and entered the bay near site C. From site C they turned eastward and spread into the area east of sites C, D and E, but went only a short distance into the bay. It is known that the perch remained in this area during the night because the directional counts at site C indicate that they entered the bay during each presunset peak and left the bay at each sunrise peak. The perch did not go much farther into the bay than sites E and F as shown by the marked decrease in the rate of capture of perch and the lapse of time between the peaks at successive sites along the migration route. The measurements of length and weight, the scale samples, the regularity of the time of the migration and the consistently large numbers indicated that the same fish were involved in the migration each day. The sunrise migration of the perch followed approximately the same route but travelled in the opposite direction.

Shift of Peaks According to Sunrise and Sunset

The various net settings at sites B and C during 1952 are presented in Figure 4. Considering site B first, it is seen that the presunset peak ended abruptly at sunset even though sunset was more than an hour earlier in September than it was in

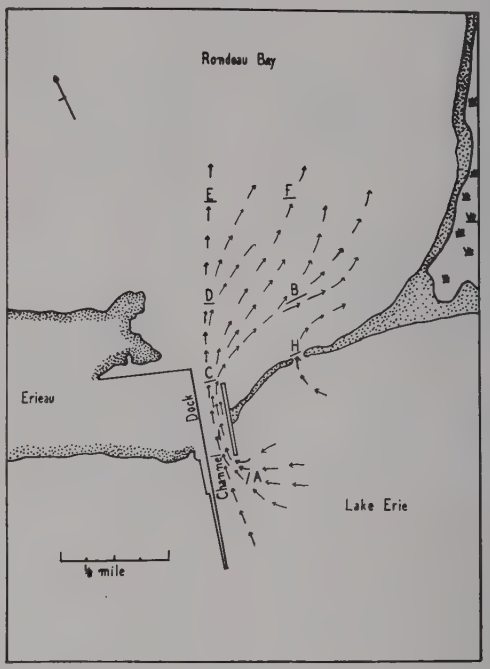

FIG. 3. Route of the presunset migration of perch into Rondeau Bay.

June. When the nets were lifted hourly during the peaks, in no case was a sufficient number of perch caught from one hour after sunset to one hour before sunrise to permit them to be plotted on the scale used. The sunrise peak normally started quite suddenly, built up higher and then tapered off so that the migration was practically over about three hours after sunrise. At site C the presunset peak ended an hour before sunset and thus an hour before the peak at site B. The sunrise peak at site C did not begin until nearly an hour later than at site B. These differences are again explained by the daily migrations of the perch from the bay to the lake and back. Weather observations taken at each lifting indicated that the sunrise peaks were later than usual and the presunset peaks were earlier than usual when the sky was cloudy.

Analyses of Stomach Contents

The analyses of stomach contents of perch caught in 1½-inch mesh nets during 1952 showing the chief types of food are presented in Figure 5. Cladocerans formed the largest food item by volume and the volume of fish eaten was only slightly less. Insects and small crustaceans (other than cladocerans) were represented in smaller

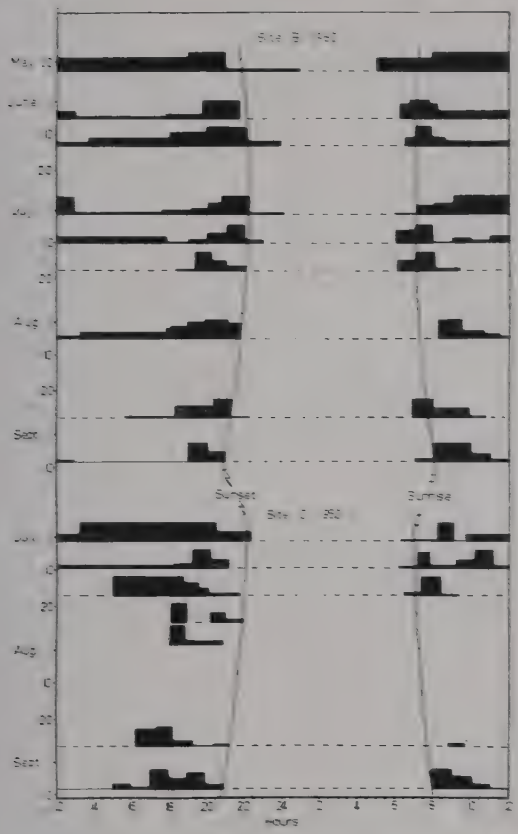

FIG. 4. Change of the peaks at sites B and C with the change of the times of sunset and sunrise.

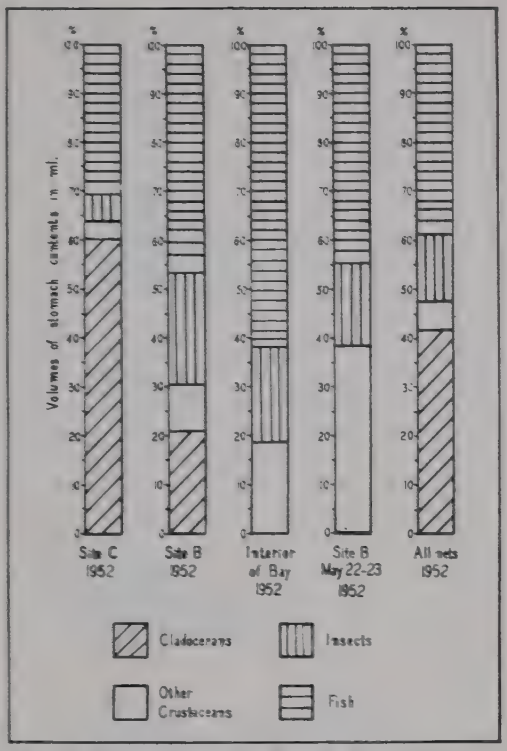

FIG. 5. Composition of the food of perch. Sites B and C represent migratory perch while the interior of the bay represents non-migratory perch.

volumes. The cladocerans were entirely *Daphnia pulex* (de Geer) except for three stomach samples containing *Leptodora kindtii* (Focke). A single specimen of *Cyclops* was found. The fish eaten by the perch were 95 per cent minnows and 5 per cent young perch. Of the insects mayflies made up 68 per cent and caddisflies formed 18.5 per cent. Of the crustaceans other than cladocerans, crayfish and amphipods were the important forms. The average volume of the contents from 714 stomachs from site C was 0.417 ml. and the average volume of the contents from 767 stomachs from perch at site B was 0.322 ml. The average volume from 253 stomachs from the interior of the bay, representing non-migratory perch, was 0.189 ml.

At sites A and C, *Daphnia* formed the largest volume of food but at site B they played a much less important role. In the interior of the bay the cladocerans were practically absent from the perch stomachs. The reason for this was made obvious by the series of surface and bottom plankton samples at site B on two days in August, 1951. A total of 7 *Daphnia* were obtained from 240 liters of water containing 7180 crustacean plankters. A study of plankton in Rondeau Bay by Miss M. Prouse in 1953 has shown that *Daphnia* are very scarce in the interior of the bay but are plentiful in the inshore waters of Lake Erie. Thus the stomach analyses provided a means of distinguishing between the migratory and the non-migratory perch since only the migratory perch could feed upon *Daphnia*.

The average volume of cladocerans in perch stomachs during the various hours of the day at sites B and C is presented in Figure 6. Time periods containing less than five stomachs were not plotted. Immediately below each graph of the volumes of the cladocerans is the number of perch stomachs with some food which were sampled during the period. The large peak in the average volumes of cladocerans occurred earlier and was of a much greater magnitude at site C than at site B. This is partly explained by the fact that the cladocerans were eaten in the lake during the day and on the return to the chan-

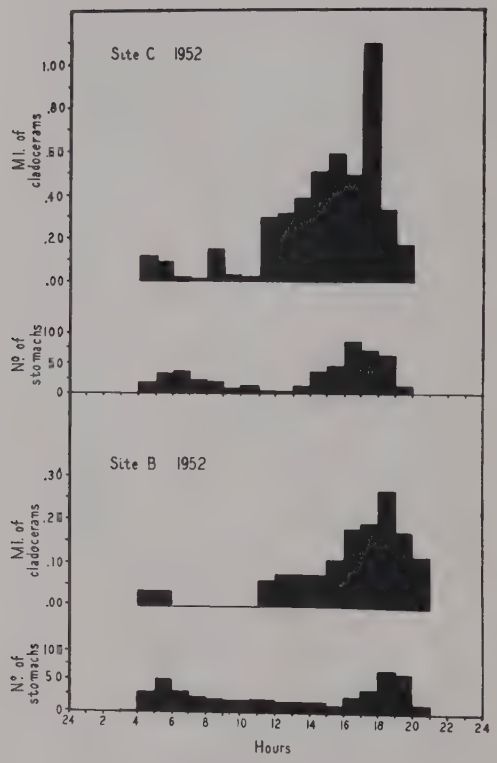

FIG. 6. Average volume of cladocerans in perch stomachs at various hours.

nel. After entering the channel and the bay the perch fed on other food items and the peak in the average volume of cladocerans moved from site C to site B as the main body of the migrating perch moved into the bay.

It should also be noted that at sunrise there was no peak in the average volume of the cladocerans at site B since there are practically no cladocerans in this region for the perch to feed on. When the migratory perch reached site C there was only a slight peak in the average volume of cladocerans. The average volume of cladocerans remained at low level until the beginning of the return migration during the presunset peak.

DISCUSSION

In order to correctly interpret Figure 2 it must be remembered that a change in the rate of capture of fish may be caused by a change in the local abundance of the fish or a change in the activity of the individual. The rate of capture of non-migratory fish is an index of their activity but the rate of capture of migratory fish is affected by both the activity of the individual and the local abundance of the species.

At sites B and C, the decrease of the catch during the sunrise peak was due to a decrease in local abundance rather than a decrease in activity since a migration to the lake at this time was established. The increased rate of capture during the presunset peak was due to the increase in local abundance when the perch returned to the bay. The decrease in the rate of capture of perch at sunset and the increase at sunrise were due to changes in the activity of the fish since there was no change in the local abundance between sunset and sunrise. Thus the small catches at midday were due to the local scarcity of perch while the very small catches at night where due to their inactivity.

The avoidance of nets by fish is probably greater during daylight hours since the nets become more readily visible but it does not account for the large changes observed. This was indicated best by the activity pattern of the pumpkinseed, *Lepomis gibbosus* (Linnaeus), (not presented) which had a marked peak of activity during midday. The non-migratory perch (Fig. 2h) also showed larger catches during daylight hours, indicating that avoidance of nets could not have produced the effects observed at sites B and C.

The analyses of the stomach contents showed striking differences in the food eaten by the migratory and the nonmigratory perch. *Daphnia* formed the largest volume of food of the migratory perch but were nearly absent from the stomachs of the non-migratory perch. A larger proportion of *Daphnia* were present in the stomachs than in the plankton samples suggesting that the perch may feed selectively on them. Since they were scarce in the bay it suggests that the migration may serve the function of obtaining this food item.

The first stomach analyses of the season taken on May 22-23 (Fig. 5) differed from all subsequent samples from the same site in that *Daphnia* were almost absent. As other investigations have shown that they were scarce in the lake at that season and since the activity pattern remained that of migratory perch, it was concluded that the perch were migrating into the lake in May. It was found that the perch were still performing the migration in early October but it was not known whether the migration continued through the winter. The daily migrations of perch in Lake Mendota took place during the summer only (Hasler and Bardach 1949).

Summary

In Rondeau Bay, perch, *Perca flavescens* (Mitchill), were the most abundant fish large enough to be caught by gill-nets. In summer the two chief groups of perch were (a) two- and three-year-old migratory perch which were concentrated at the end of the bay nearer Lake Erie and migrated daily into the lake and (b) two- and three-year-old non-migratory perch remaining in the interior of the bay.

The activity patterns, as measured by gill-net catches, indicated that all the perch were very inactive during the hours of darkness. The catches of migratory perch showed daily sunrise and sunset peaks. The low catch during midday was due to decreased local abundance. The non-migratory perch became active at sunrise, showed a peak of activity at about 1700 hours, and became inactive after sunset.

An approximate route of the daily migration of perch between Rondeau Bay and Lake Erie is presented. The migration was detected chiefly by tabulating the direction in which the perch were headed when caught in the net, by a chronological succession of peaks along the migration route and by analyses of the stomach contents.

Light appeared to play an important role in the timing of the beginning and ending of the day's activity. The time of the migration changed with the change in the time of sunrise and sunset during the season.

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AN APPROACH TO THE PALEOECOLOGY OF MAMMALS

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Introduction

The paleoecology of Tertiary invertebrates and plants has been widely and effectively studied by applying the uniformitarian concept in comparison of living and fossil species. This approach makes use of the occurrence in Tertiary deposits of species which are essentially the ecological equivalents of those now living, as judged from their close morphological similarity. Paleobotanists have applied this most successfully to community groupings (the work of R. W. Chaney and students for example), whereas the invertebrate paleontologist has more often used one or more stenotopic forms to indicate environmental conditions (Smith 1919; Durham 1950). This method of reference to living environments has provided data concerning changes in distribution of faunas and floras which are interpreted as reflecting climatic changes. The fact that invertebrates and plants had established their adaptive radiations by or soon after the beginning of the Tertiary makes such an approach possible.

Mammals, however, had only begun their adaptive radiation by the beginning of the Tertiary. Most living families of mammals are not known before the Oligocene and few living genera are known before the Pliocene. It is obvious then, that the approach of the invertebrate paleontologist and the paleobotanist cannot be applied in the determination of the paleoecology of mammals. These fields of study, especially floristic paleobotany, however, offer much information to the student of fossil mammals regarding climate and, to a lesser extent, the topographic diversity during Tertiary time.

The rapid evolution and adaptive radiation of mammals in the Tertiary has presented an enigma to the mammalian paleontologist as to criteria for an approach to the paleoecology of mammals. Some use has been made of morphology alone as suggesting environmental situations. Community structure, though, cannot be approached in this way without a background of criteria based on quantitative analysis of quarry samples.

Acknowledgments

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Illustrations are by the author.

The Quarry as a Source of Quantitative Data

Localized concentrations of fossil bones often occur in the sediments. These concentrations make excavation on a large scale practical, and are referred to as quarries. They vary greatly in the density of materials and in total volume. Such concentrations often furnish a large number of specimens which in varying degree represent the fauna once living locally. The nature of this representation must first be determined in order to make use of the quanitative data available.

Many quarry samples obviously do not present a true picture of the fauna they represent. This may be indicated by the presence of only one species in the sample. The *"Stenomylus"* and *"Coryphodon"* quarries are examples of this. A sample may also be useless in which only one ontogenetic age group is present. Another questionable type of quarry sample, for our purposes here, is that in which there is a strict selection of size of individuals included. These are sometimes explained as carnivore lairs. Other quarry samples may be more diverse in forms and age groups. The nature of their representation is more subtle.

In living mammalian faunas a general relationship is evident between the number of carnivores (individuals) and herbivores present in a given area. This relationship is often referred to as the "Eltonian Pyramid." The herbivorous mammals form the base of the pyramid with the lesser number of carnivores making up the upper part of the pyramid. This represents a generalized food-energy cycle controlling the balance in a fauna. Presumably these restrictions in food-energy cycles are transferable to fossil faunas. We can use this as a rough indicator of balance in a fauna. If a quarry sample, supposedly a large enough one, does not indicate the gross balance in the fauna it cannot be considered as a true representation of the fauna. On the other hand if the sample appears to show the balance of numbers of herbivores and carnivores which was present in the original living fauna then it presents the most desirable quantitative data for a study of the paleoecology it represents. As an example the relative number of individuals of herbivores and carnivores for the two faunas employed in the approach outlined here, McKay Reservoir and Hemphill, and those of Rancho LaBrea are illustrated in Figure 1. It is readily seen that the Rancho LaBrea figure does not indicate the necessary balance of the fauna in the sample whereas those from the other two faunas do reflect this balance. They appear, at least in a broad way, to provide a more probably true quantitative representation of the living fauna they were originally derived from.

Problems Involved in the Quarry Sample

Even after the quarry sample is determined to be a likely true quantitative representation of the once living fauna, other problems arise as to its possible errors in representation.

Forms which are nearly always rare or missing in fossil mammalian faunas, irrespective of their probable abundance in the area, are those with volant or arboreal habits. This characteristic has hindered the study of such groups as bats, primates, and flying squirrels. Their usual small size and fragility does not seem to be the important factor since insectivores and small rodents are not uncommon in quarries. Their habits which keep them away from sites of deposition more than other mammals must be responsible. Other forms may not be found in the quarry sample due to their low density in the area supplying material to the deposit. A paleontologist can never expect to have a complete faunal list.

It may be of interest at this point to make an estimate of the completeness of our faunal lists. The faunas used in the present study are assigned to the Hemphillian Provincial Age (about mid-Pliocene.) Paleobotanical evidence indicates that our present diversity of environments was becoming established by Hemphillian time. The diversity of Hemphillian mammals as shown in numbers of genera might be expected to be roughly equal to the number of living genera. This allows for additions due to increasing diversity and subtractions brought about by migration and extinction. It is necessary in such an estimate to rule out forms which we know are usually poorly represented, arboreal and volant, in order to obtain a comparative estimate. The fossil evidence of Hemphillian mammals for North America is almost completely restricted to the United States so that the numbers of living genera used in the

FIG. 1. Relative numbers of individuals of carnivores to herbivores in the McKay Reservoir local fauna, the Coffee Ranch quarry of the Hemphill local fauna, and the Rancho LaBrea local fauna. Data for Rancho LaBrea from Stock 1939.

estimate are those found in the United States. Table I lists the number of genera of living and Hemphillian mammals by orders. The classification used is that of Simpson (1945).

Ninety-one living genera of mammals are listed. This includes thirteen genera of bats. When these are removed there remain seventy-eight genera.

TABLE I. *Numbers of Recent and Hemphillian Genera of Mammals*

Order	Recent	Hemphillian
Marsupialia	1	0
Insectivora	10	2
Chiroptera	13	Unassignable material
Edentata	1	1
Lagomorpha	4	4
Rodentia	34	21
Carnivora	17	19
Proboscidia	0	3
Perissodactyla	0	6
Artiodactyla	7	11
Total	91	67

The table shows a total of sixty-seven genera of Hemphillian mammals.

If the number of living genera of mammals is an indication of the number of fossil mammals to be expected to have lived in the same general area and in a similar diversity of environments, then the recovery of fossil mammals, Hemphillian age at least, is more complete than is usually assumed (about 85% in this example.) This, of course, means completeness of a faunal list, not quantitative completeness. Following the same comparative method used for the entire U. S. Hemphillian fauna a rough estimate of the same type may be made for local faunas. The data for the number of living genera is derived from descriptions of local faunas of various parts of the United States. These are usually lists of the mammals of some small county, a game reserve or research reserve. The number of genera averages about 30-35. The number of genera appearing in the two faunas which are used in this study are 22 and 28. This represents about the same degree of completeness as was evident when considering the entire United States fauna. Admittedly this is a rough estimate but if the method used in obtaining it is reasonable, then the results are of interest, much more so than the usual subjective remarks offered.

Another problem common to many quarries centers around the fact that quarries frequently contain representatives of more than one community. These community mixtures are so common that a special term has been used for them, the "Thanatocoenosis," suggesting that only in death are these organisms found together. In any approach to the paleoecology of any group of animals or plants there must be a separation of these communities.

Chaney (1924), working with leaves, has compared quarry accumulations at the Bridge Creek flora localities and those accumulating at present in a number of small depositional basins in Muir

Woods, California. The plant association at Muir Woods compares closely with that of the Bridge Creek flora. His results indicate that there is a high correlation between the number of plants locally present of a given species, and the number of leaves of that species present in the basin. A high incidence of leaves of a species indicates then, proximity of that species to the site of deposition. The relative abundance of leaves of various species in the accumulating deposits at Muir Woods is similar to those from the quarry at the Bridge Creek locality. Although the actual mechanics of transportation of leaves to the depositional site and their preservation are not the same as those for mammals, it is probable that there is a corresponding relationship between the materials preserved and the once-living associations. The leaves of some species of woody plants do not occur in deposits except in rare instances because of the structure of the leaf. This selection, due to structure, seems not to be evident in mammals.

It can be seen that even in quarry samples which by broad standards appear to represent well the fauna they are derived from there are a number of inherent misrepresentations. These may be listed as:

1. A quarry sample does not produce a complete faunal list of any of the communities represented.
2. Often more than one community is represented in a quarry.
3. Materials are perserved in the quarry in relation to the habits of the species, density of the species in the area and proximity of the the species habitat to the site of deposition.

The present method, in part, makes use of some of these "misrepresentations" to derive an interpretation of the quantitative data available. For instance, it was suggested above that some separation of communities may be possible by determining proximity of the habitat of a mammal to the site of deposition. It will be seen below that the mechanics for doing this are largely based on the apparent quantitative misrepresentations in the sample.

Method of Collecting the Sample

The method used in obtaining the quarry sample is the most important part of any quantitative analysis. The sample must be assumed to have been taken at random. The collection of material then must be made so that every specimen in the volume of sediment worked is retained. This includes every scrap, not just complete or nearly complete material. Collecting only the anatomically complete material from quarries of course makes results useless for an ecological quantitative analysis and certainly cannot be considered valid for quantitative morphological analysis. In fact, this practice has already destroyed the possibility for any type of quantitative analysis in many North American Tertiary faunas. The sample collected from McKay Reservoir, Oregon, the principal fauna used in this approach, was made by working small blocks of wet sediment by hand. The light-colored specimens were easily distinguished from the dark sediments which made possible a high percentage of recovery. The Coffee Ranch quarry sample (Univ. Calif. Coll.) of the Hemphill Fauna (Texas), used in the contrast of faunas below, was collected with care to recover all material present. The McKay Reservoir sample includes 751 specimens while the Hemphill sample includes 3,259 specimens.

Approach to Proximity and Density Problems

If a species of mammal is a member of a community in close proximity to the site of deposition, individuals may be expected to have died more often near the site of deposition and thus become a part of the accumulating deposit than those of a species which lived in a distant community. Species are excluded which, owing to their habits, are not commonly preserved (volant or arboreal forms). Mammals from distant communities appear in the deposit as materials introduced by the activities of carnivores, by stream action carrying them in, or by some other method of chance occurrence. They may be expected to be represented by fewer bones of their skeleton per individual present simply because they have less opportunity of being completely preserved. As a corollary, it is assumed that the completeness of representation indicates the proximity of the habitat of the species to the site of deposition.

When there are few or no articulated specimens in a sample it is not possible to determine exactly the number of individuals of a species represented. A useful indication can be found by determining the smallest number of individuals which could produce the material present. This *minimum number* is arrived at by examining all the material referable to each species, fragmental and complete, noting the element present most frequently. Thus fragments or complete specimens of five femurs of a species, three lefts and two right, demand three individuals as the minimum number represented. In some instances the most frequent element may not be the deciding one, for instance in the example above, if there had been

four tibia, all lefts, it would have been necessary to allow four individuals as the minimum number. The element used may be any recognizable part of the skeleton, teeth, limb elements, or skull fragments.

Another quantity that can be useful from the data of each species in the deposit is the *number of specimens* which represent it in the sample. This should not be confused with the minimum number. The *number of specimens* is simply the number of recognizable bones and teeth which are present in the sample. For instance, in Table III it is indicated that the number of specimens of *Osteoborus* in the Hemphill sample is 362. However it is only necessary to propose 15 individuals (the minimum number) to account for these specimens. A ratio of the two numbers

$$\left(\frac{\textit{number of specimens}}{\textit{minimum number}}\right)$$

gives the number of specimens per individual and thus an indication of the relative completeness of preservation when applied to a number of species.

A difficulty in this approach lies in the variation of the number of skeletal elements to be found in different genera of mammals. For instance, a rhino may be expected to contribute more recognizable elements to a deposit than a horse (that is, later Tertiary horses) owing to the larger number of foot elements in the rhino. It may also be expected to produce more elements than a small rodent. The rodent has a similar number of elements, but rodent foot bones are difficult to assign. There is therefore a variation in the *number of specimens* due to the difference in the number of skeletal elements various mammals can contribute and also to the difference in the number of skeletal elements which the worker can readily assign. In order to eliminate such variation, the data should be corrected so that the *corrected number of specimens* represents the number which would be expected if all genera contributed the same number (the *standard number of elements*) of recognizable elements. This is done by setting up the following proportion:

$$\textit{Corrected number of specimens} = \frac{\textit{number of specimens} \times \textit{standard number of elements}}{\textit{estimated number of elements}}$$

The *estimated number of elements* for a genus is arrived at by determining how many elements the worker could distinguish for each genus involved if all its different elements were available. In the present approach ribs and vertebrae, which do not show much variation in numbers between groups of mammals, were not considered or counted.

The determination of the *estimated number of elements* for the pika (*Ochotona*) of the McKay Reservoir, Table II, appears to be a special case. Its *minimum number* is 11, the same as for *Hypolagus*. However, the number of specimens representing *Ochotona* is only 17 while that for *Hypolagus* is 203. Examination of the pika material shows only elements of the head to be present in the sample. A careful search of all the small mammal material reveals no elements of any other part of the skeleton to be present. It seems, at least in this case, that there is reason to believe that the rest of the skeleton was destroyed at the time of death. Perhaps the pika's predators, owls, canids or some other carnivore which takes in the whole body found the head of the pika obstructive or for some other reason disgorged it when the pika was killed. Whatever the cause it is too frequent an occurrence in this case to be considered as a matter of chance. For this reason the *estimated number of elements* of the pika is much lower than for any of the other mammals listed.

The *standard number of elements* is completely arbitrary since any number should give the same results. In this example fifty-seven was used be-

TABLE II. *McKay Reservoir Quarry Sample*

Genus	Number of individuals	Relative abundance	Number of specimens	Estimated no. elements	Corr. no. specimens	Specimens per individual
Scapanus	1	1.1	2	23	5.0	5.0
Desman	2	2.3	7	23	17.3	8.7
Chiropterid	1	1.1	2	15	7.6	7.6
Ochotona	11	12.5	17	7	138.2	12.6
Hypolagus	11	12.5	203	45	257.1	23.4
Liodontia	1	1.1	1	41	1.4	1.4
Marmota	2	2.3	3	41	4.2	2.1
Citellus (O)	5	5.7	25	41	34.8	7.0
Citellus (C)	1	1.1	1	41	1.4	1.4
Pliosaccomys	2	2.3	4	23	9.9	4.9
Perognathus	1	1.1	1	23	2.5	2.5
Geomyid	1	1.1	1	23	2.5	2.5
Dipoides	14	15.9	219	41	304.4	21.6
Microtid	1	1.1	4	23	9.9	9.9
Pliozapus	2	2.3	2	23	4.9	2.5
Plesiogulo	1	1.1	2	75	1.5	1.5
Felis	1	1.1	5	75	3.8	3.8
Machairodus	1	1.1	5	75	3.8	3.8
Osteoborus	1	1.1	7	75	5.3	5.3
Canis	4	4.5	34	75	25.8	6.4
Martes	1	1.1	1	75	0.8	0.8
Hipparion	3	3.4	10	81	7.0	2.3
Neohipparion	1	1.1	1	81	0.7	0.7
Teleoceras	4	4.5	108	126	49.3	12.3
Paracamelus *Procamelus*	3	3.4	16	57	16.0	5.3
Prosthennops	11	12.5	69	79	49.8	4.5
Proboscidian	1	1.1	1	49	1.1	1.1

cause it was about median in the range of the *estimated numbers of elements* for the mammals in the sample. The use of a median number in the range of the estimated numbers of elements as a *standard number of elements* has the advantage of keeping the amount of correction to a minimum, some genera requiring no correction at all (those with an *estimated number of elements* of 57). The *estimated number of elements* will vary with different authors. This difference however will probably not present any appreciable source of error in the approach here presented.

An illustration may help to clarify the operation described above. *Hypolagus,* in the sample from the McKay Reservior fauna (Table II) is represented by 203 specimens (*number of specimens*). The *estimated number of elements* for the genus is determined as 45. Using 57 as the *standard number of elements* the

$$\text{Corrected number of specimens} = \frac{203 \times 57}{45} = 257.1$$

The results of the determination of the *corrected number of specimens* for each of the mammals found in the samples from McKay Reservoir and the Hemphill are included in Tables II and III. Also included are the *numbers of specimens per individual* for each genus. This figure is the result of the division of the *corrected number of specimens* by the *minimum number* (number of individuals.) It is an expression of the completeness of preservation of each species in the sample. It should be remembered that relative completeness of preservation is assumed, in this approach, to be an indication of the proximity of the habitat of a mammal to the site of deposition.

TABLE III. *Hemphill Fauna Quarry Sample*

Genus	Number of individuals	Relative abundance	Number of specimens	Estimated no. elements	Corr. no. specimens	Specimens per individual
Sloth	2	1.3	5	87	3.3	1.5
Hypolagus	3	2.0	24	45	30.4	10.1
Mylagaulus	3	2.0	16	29	31.5	10.5
Canis	1	0.65	10	75	7.6	7.6
Osteoborus	15	9.9	362	75	274.5	18.3
Plesiogulo	1	0.65	2	75	1.5	1.5
Vulpes	2	1.3	18	75	13.7	6.8
Agriotherium	1	0.65	11	75	8.4	8.4
Machairodus	3	2.0	108	75	82.1	27.3
Aphelops	9	5.9	374	126	169.0	18.8
Telecceras	1	0.7	1	126	0.5	0.5
Nannippus	5	3.3	191	81	134.0	26.9
Neohipparion	3	2.0	126	81	88.7	29.4
P. Astrohippus	7	4.6	224	81	157.4	22.5
Pliohippus	63	41.5	1157	81	815.0	12.4
Prosthennops	5	3.2	65	79	46.9	9.4
Pediomeryx	3	2.0	40	57	40.0	20.0
Capromeryx	2	1.3	42	57	42.0	21.0
Pliauchenia	21	13.8	416	57	416.0	19.8
Paracamelus	3	2.0	37	57	37.0	12.3
Alticamelus	3	2.0	22	57	22.0	7.3
Proboscidian	2	1.3	8	49	9.3	4.7

The data in Tables II and III which are to be used in the remainder of the discussion are the *relative abundance* (based on *minimum number*) and the *number of specimens per individual.* These data are presented graphically in what are called here *faunal analysis diagrams.* (Figs. 2, 3.) These diagrams consist of a circle graph divided to represent the relative abundance in the sample of the mammal indicated. These divisions are blacked in with a radial bar graph which shows the number of *specimens per individual* for the same mammal. The members of the fauna are arranged counterclockwise on the diagram in the decreasing order of their *number of specimens per individual,* or in other words, as assumed in this approach, their order of proximity to the site of deposition.

In order to designate the community of genera which are not common to both faunas it is necessary to delimit the proximal community on the faunal analysis diagram. The point at which the average *number of specimens per individual* occurs on the diagram is used here as the limit of the proximal community. It is noted on the diagrams by a heavy concentric line which includes all of its members appearing in the sample. Earlier it was assumed that completeness of preservation, measured by the number of specimens per individual, is an indication of proximity of the habitat of a mammal to the site of deposition. Mammals must then have a higher-than-average *number of specimens per individual* to be considered as members of a proximal community. Those below average belong to intermediate and distant communities.

In faunas representing different environments those mammals in common to both faunas, which appear as members of the proximal community on the faunal analysis diagram of one of the faunas cannot in most cases be expected to appear in the proximal community of the other fauna. This characteristic presents a method of evaluating some of the assumptions upon which the interpretation of the faunal analysis diagram is based. If the interpretation of the diagrams of faunas of different environments based on the assumptions presented earlier bears out the necessary mutually exclusive nature of most of the members of the association of the proximal community then it may be said to form a reasonable working hypothesis for an approach as presented here. A test is made below using the McKay Reservoir, Oregon and

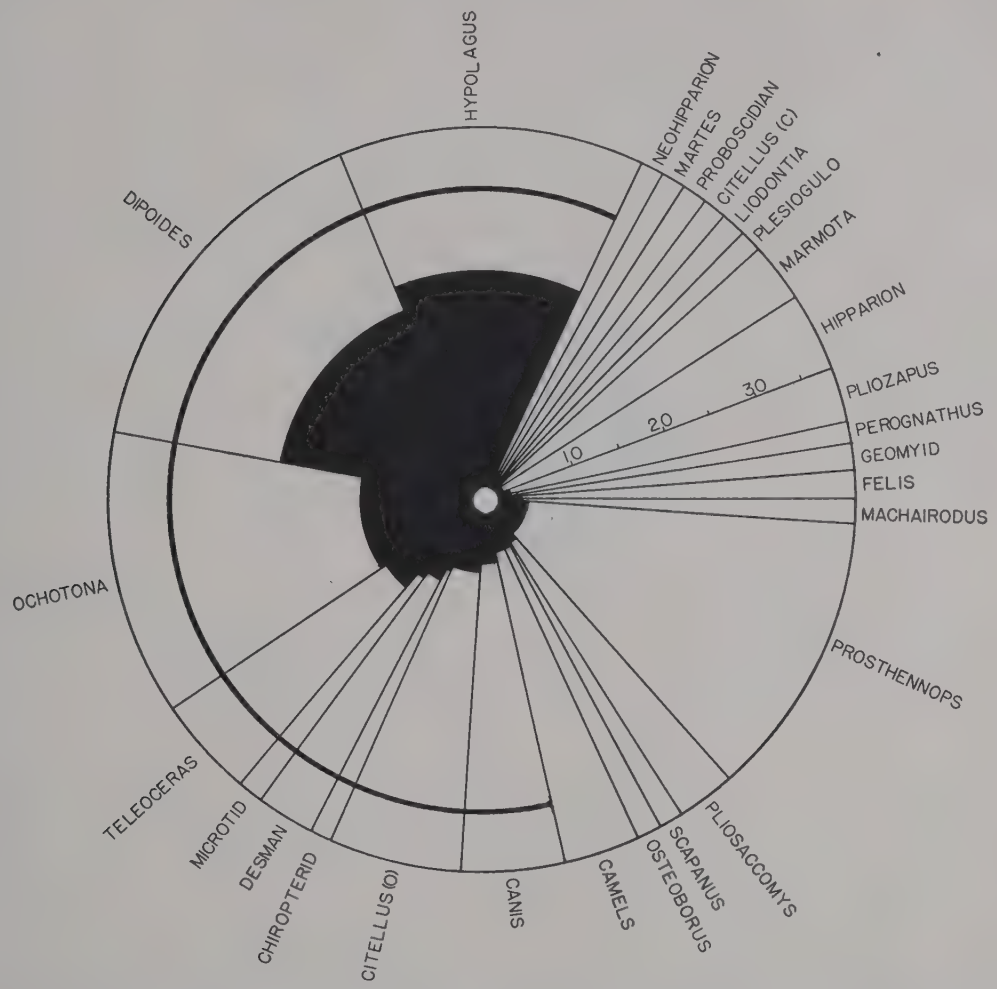

FIG. 2. Faunal Analysis Diagram of the quarry sample from McKay Reservoir, Oregon. The divisions of the circle graph represent relative abundance of the mammals indicated. The radial bar graph represents the number of specimens per individual. The heavy concentric line includes genera assigned to the proximal community.

Hemphill (Coffee Ranch) Texas quarry samples. These two faunas are contemporary by present standards of correlation. They both contain a number of short-lived genera (in geologic time). Although there are a number of mammals common to both faunas, as known from the quarry samples, the faunal lists of the two are otherwise quite different. Since these are essentially contemporary faunas the difference expressed is likely due to environmental differences at the two sites of deposition at the time these animals lived. Other evidence which might be obtained from plants in association with the mammals in the sediments is not available. Such associations occur only rarely. However, Chaney and Elias (1936) have shown that the Great Plains environment was well established by the time of the Hemphill Fauna. Chaney (1944) has shown also that at the same time the environments of the Pacific Coast were becoming more diverse. It seems probable then that the gross differences in the McKay Reservior and Hemphill (Coffee Ranch) faunas are due to their existence under different local environmental conditions.

Using the McKay Reservoir and Hemphill faunas illustrated in the diagrams (Figs. 2, 3) we note that nine genera of mammals are found in both faunas. Six of these appear on the diagrams as members of proximal communities. These are *Neohipparion* (horse), *Machairodus* (saber-

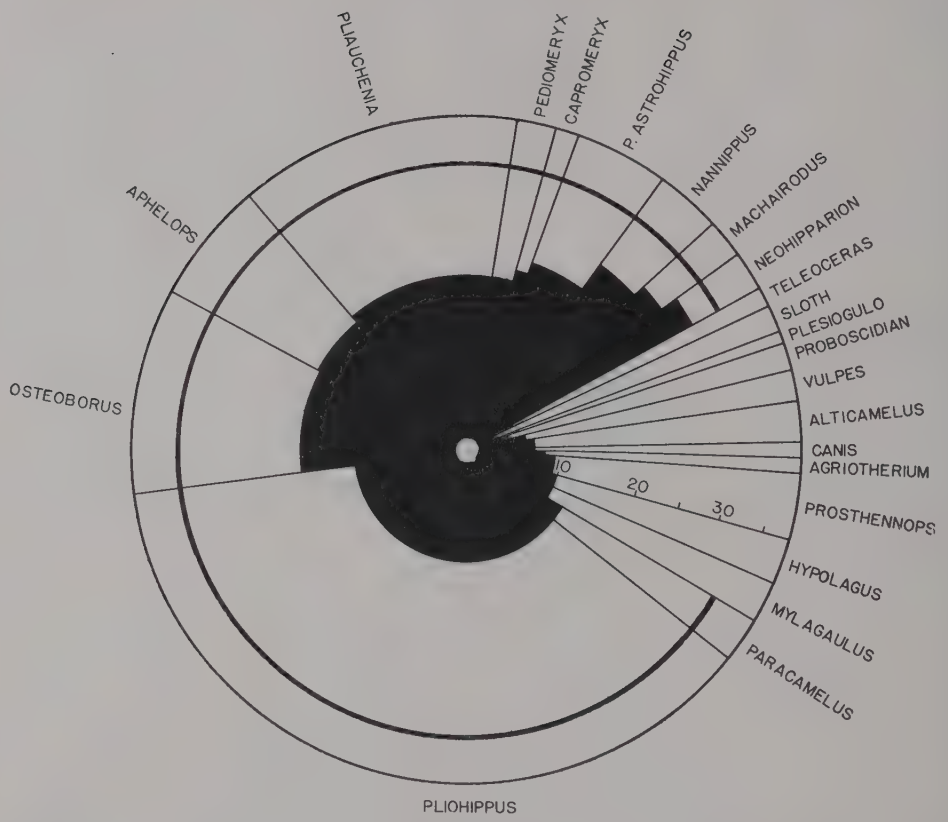

FIG. 3. Faunal Analysis Diagram of sample from the Coffee Ranch quarry, Hemphill local fauna, Hemphill County, Texas.

toothed cat), *Osteoborus* (hyaenoid dog), *Paracamelus* (camel), *Hypolagus* (rabbit) and *Teleoceras* (rhino). *Neohipparion, Machairodus, Osteoborus* and possibly *Paracamelus* are representatives of the proximal community in the Hemphill (Fig. 3) but these mammals represent distant communities in the McKay Reservoir fauna (Fig. 2.) *Hypolagus* and *Teleoceras* are members of a proximal community at McKay Reservoir (Fig. 2) but are in more distant communities at Hemphill. These are the results which are to be expected if the assumptions upon which the interpretation of the faunal analysis diagram is based are valid. Apparently they are, at least as far as this evaluation can test them.

The relative abundance of the various members of the proximal community as they appear on the faunal analysis diagram are probably indicative of their relative density in the once living fauna. These relative abundances are shown on the diagrams (Figs. 2, 3) by the size of the division of the circle. The data for mammals of distant communities, of course, have little relationship to their relative densities in their home community since they appear in the quarry sample as only chance occurrences. It is interesting to note the implications of the relative densities of various forms in the proximal communities. In the Hemphill (Fig. 3) for instance, *Machairodus* (saber-toothed cat) has a very low density, while *Osteoborus* (hyaenoid dog) on the other hand is a much more common form. Possibly *Machairodus* was a solitary animal or worked in pairs, whereas *Osteoborus* traveled in packs. The hipparion horses (*Nannippus* and *Neohipparion,* three-toed) and the smaller pliohippine horse (*P. Astrohippus,* single-toed) are of low density while the large pliohippine horse (*Pliohippus,* single-toed) is the most common form in the community. Apparently the smaller Pliocene horse did not occur in great herds here but the larger ones did. A realization of the relative densities of various mammals as

expressed in the faunal analysis diagram may be helpful in studies of their taxonomic evolution.

Habitats of the Proximal Communities

When it is necessary to determine the nature of the habitat from the mammalian material alone, the best source of such information is the functional morphology of all the inhabitants of the community. The members of the proximal community appearing in the quarry sample from McKay Reservoir are listed below.

McKay Reservoir

Hypolagus (rabbit)
Dipoides (beaver)
Ochotona (pika)
Teleoceras (rhino)
microtid
desman mole
bat
Citellus (O) (ground squirrel)
Canis (small dog)

Among these are several mammals which are probably aquatic or amphibious. They are the desman mole, the beaver (*Dipoides*), and the amphibious rhino (*Teleoceras.*) Some type of large pond or small lake must be suggested to provide the habitat for these forms. The presence of ducks, crayfish and amphibians in the fauna further emphasizes the presence of a body of water. Presumably this body of water was the site of deposition of the materials which make up the quarry. The other members of the proximal community consist of rodent and lagomorph grazers. The habitat of the proximal community then appears to have been a pond-bank association.

The Hemphill proximal community is as follows:

Hemphill

Machairodus (saber-toothed cat)
Neohipparion (three-toed horse)
Nannippus (small three-toed horse)
P. Astrohippus (small single-toed horse)
Capromeryx (antelope)
Aphelops (rhino)
Osteoborus (hyaenoid dog)
Pliohippus (large single-toed horse)
Pediomeryx (large deer-like mammal)
Paracamelus (large camel)
Pliauchenia (small camel)

The Hemphill proximal community consists of a number of large grazing herbivores that are characterized by high crowned teeth and lengthened metapodials. The other members of the community are their large predators. This group of mammals represents a grassland habitat.

After the listing of the members of the two proximal communities there still remain eighteen mammals in the two quarry samples which do not appear as members in either proximal community on the faunal analysis diagrams. Three of these occur in both faunas. They are *Prosthennops* (peccary), *Plesiogulo* (wolverine) and the proboscidian. These three may represent an environment intermediate to those represented by the proximal communities. The others may not appear on the faunal analysis diagram as members of a proximal community because they also represent an intermediate environment, they may appear as they do as results of sampling error, or they may be low-density forms of one of the proximal communities that do not appear as such due to random sampling. Probably all three of these suggestions account for the fifteen unassigned mammals. A logical intermediate environment between a grassland and pond-bank association is brush or open woodland. Many of the forms considered have morphologies indicative of such an environment. These are omnivores, browsing herbivores and small carnivores. It will be necessary however to collect a quarry sample which has a proximal community habitat of an open woodland to determine the proper assignment of mammals to such an environment.

Distribution of Habitats Locally

In the discussion above it was concluded that three major habitats were indicated. These were pond-bank association, grassland, and an intermediate open woodland. At both quarries all three habitats were recognized as either a proximal, distant or intermediate community in relation to the site of deposition. These quarry samples from contemporary faunas can then be considered as ecofacies of the total fauna of the time. Figure 4 is an illustration of a possible distribution of the habitats and sites of deposition which would produce the results described.

Summary

The approach to the paleoecology of mammals presented here is based on the following assumptions:

1. Reasonably large collections from quarry accumulations are a random sample of what is present in the quarry providing all specimens are retained from the volume of sediment worked.
2. An indication of density of mammals of the proximal community may be obtained from use of the *minimum number*.
3. Mammals whose community in life was close to the site of deposition will be more com-

FIG. 4. Geographic relationship of community habitats. (a) Site of deposition of the ecofacies type which appears as the proximal community at McKay Reservoir. (b) Site of deposition of the ecofacies type which appears as the proximal community of Hemphill.

pletely represented than will those whose community was farther away.

4. If a community other than the proximal one is represented in a quarry sample, the habitat of that community must be present in the region contributing specimens to the quarry.

These assumptions form the basis for the interpretation of the quantitative data presented by the quarry sample. They are in part tested by applying the interpretation to the data of two faunas of different environments. The result demonstrates the necessary difference in membership of the proximal communities. It is felt therefore that the interpretation and the assumptions upon which it is based form a reasonable working hypothesis for studying the paleoecology of mammals. The advantage of this approach is that it not only indicates the habitat various fossil mammals lived in but determines their relative density in their community, lists other members of the community, separates the several communities represented in a quarry and suggests the geographic relationships of the habitats in which the communities are found.

Climatic conditions are not found by this approach except in so far as the limitations of the general habitat type demand. Mammalian morphology is of little help in the determination of temperature ranges, rainfall, topographic diversity and other pertinent facts necessary to the synthesis of a climate picture. Climate, however, is a regional characteristic, and consequently the climatic conditions implied by the occurrence of a certain habitat type may be confirmed if there are other occurrences of the same type and of equivalent age within the region. Terrestrial climatic conditions are best determined from the evidence of fossil plants. Such evidence only rarely occurs in association with mammals. Thus it is necessary to transpose information from fossil plant occurrences to those of fossil mammals. This demands strict stratigraphic control. A synthesis of data readily available from paleobotany with that derived from the application of the present approach can give a picture of fossil mammal environments, both organic and physical.

If this type of approach, an approximation at best, is applied to superimposed successions of faunas, data may be obtained to illustrate the dynamics of community change over long periods of time. Such information is rare at present. It can give the ecologist the historical background in community dynamics necessary to answer many of the questions in living biota.

The approach outlined and illustrated in this study is a preliminary suggestion. It will undoubtedly be improved by analysis of more quarry samples and constructive criticism. However, if this study encourages other workers to collect with similar approaches in mind so that they do not discard or destroy valuable fragmentary material then it will have served a good purpose. Vertebrate paleontology should present the historical background for the understanding of biogeography, evolution and ecology. It should not be the mere mechanical determination of phylogenies and stratigraphic relations, techniques

which are tools of vertebrate paleontology, not the subject itself.

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NOTES AND COMMENTS

WATER CONSERVATION IN PEROGNATHUS AND PEROMYSCUS

The ability of certain small mammals to conserve moisture is an important adaptation enabling them to live in habitats of different aridity. Presumably those capable of the greater moisture conservation would be found in the drier habitats. This paper is concerned with the amounts of water lost through lungs and skin by field-caught pocket-mice, *Perognathus penicillatus eremicus* and field-caught wood-mice, *Peromyscus leucopus tornillo* from xeric habitats near Alamogordo, Otero County, New Mexico. Included also are a few observations on fieldcaught *Peromyscus leucopus noveboracensis* from the more mesic habitat near Pinckney, Livingston County, Michigan. I am indebted to Dr. L. R. Dice for the use of laboratory space and equipment in the laboratory of Vertebrate Biology, University of Michigan.

Method

The rate of water loss from the lungs and skin was determined by passing completely dry air over a mouse at a uniform rate and measuring the amount of water added to the air by the mouse in one hour. Dry food (Dice 1934) and water were available to the mice at all times except during the experimental period when neither was offered. A mouse was placed in a small wire cage just large enough to hold it. This cage was supported over a Petri dish filled with light mineral oil and both were placed in an air-tight desiccator. Any droppings or urine sank to the bottom of the oil, minimizing evaporation. The desiccator was partially immersed in a constant-temperature bath set at 25°C. A thermometer, air intake line, and air exhaust line were fitted into the lid. A filter pump drew room air through two drying towers each containing about one-half pound of anhydrous calcium chloride, next through about ten feet of coiled copper tubing which was immersed in the water bath, and then into the bottom of the desiccator. From the desiccator top, air was withdrawn through two six-inch U-shaped tubes filled with anhydrous calcium chloride. A by-pass, fitted around the U-tubes, permitted ventilation of the chamber for about one-half hour before the experimental period.

An oil manometer, an inverted escape-type oil air-pressure regulator, and a short length of fine glass tubing (1 x 50 mm.) sealed into the air line between the drying tubes and the filter pump regulated the air flow through the chamber. Air in the desiccator was changed about every half-minute at the rate of air flow employed. Tests with desiccator empty and with a small dish of water indicated satisfactory operation. During an experiment, a light shining on the mouse kept it practically inactive after investigating its new surroundings for a few minutes. Maximum variations in temperature between experiments amounted to not more than two degrees, and in each period not more than one-half degree centigrade.

At the beginning of each test the mouse was weighed to 0.01 gram. Both drying tubes were weighed to 0.0001 grams before and after each experiment. Data were analyzed by standard methods of covariance and variance.

Results

Seven males and seven females each of *Perognathus p. eremicus* and *Peromyscus l. tornillo* were tested (Table I), but only five observations were made on *Peromyscus l. noveboracensis* (not listed in Table I). *P. p. eremicus* evaporated from the lungs and skin an average of 0.033 ± .002 cc. of water per hour or 0.803 cc. per day, and *P. l. tornillo* lost 0.097 ± .010 cc. per hour or 2.326 cc. per day, and the five female *P. l. noveboracensis* tested averaged 0.119 ± .035 cc. per hour or 2.856 cc. per day.

Table I. *Insensible Water Loss in Completely Dry Air and Body Weights of* Perognathus p. eremicus *and* Peromyscus l. tornillo

	P. p. eremicus				*P. l. tornillo*			
	males		females		males		females	
	water loss per hour	weight of mouse	water loss per hour	weight of mouse	water loss per hour	weight of mouse	water loss per hour	weight of mouse
No.	gms.	gms.	gms.	gms.	gms.	gms.	gms.	gms.
1.	.0225	16.11	.0242	13.80	.0726	39.94	.0933	33.53
2...	.0442	17.28	.0391	16.43	.1125	39.42	.1702	24.78
3...	.0339	15.98	.0499	17.86	.0659	20.92	.0886	25.26
4....	.0366	18.00	.0293	14.26	.1237	31.85	.0997	29.91
5	.0285	13.79	.0384	22.18	.0496	26.67	.0524	23.16
6	.0278	20.57	.0322	14.63	.1015	40.13	.1226	24.76
7.....	.0261	17.28	.0357	17.57	.0722	26.43	.1322	23.16
Mean....	.0314	17.00	.0355	16.68	.0854	32.19	.1084	26.37

Correlation between body weight and water evaporated was not significant, consequently the analysis was continued by means of variance of water evaporated only. The sexes within species did not differ. *Perognathus* evaporated 1.523 cc. of water per day less than *Peromyscus l. tornillo*, a highly significant difference. Time did not permit a comparable series with *P. l. noveboracensis* but from the data obtained on five females of this race, 0.530 cc. per day more water was evaporated than by *P. l. tornillo*. Significance was not tested because of the small number of mice in this series. Evaporation from *Perognathus* agrees fairly well with that reported by the Schmidt-Nielsens (1950b); however, they did not report species nor race, consequently, direct comparison is impossible. Even subspecies can differ widely in physiologic characteristics. Chew (1951) reports almost one-third more water lost by five *Peromyscus* of the same race that is reported here. Variations of this magnitude are to be expected in different populations of the same race (Lindeborg 1952).

New Mexico in the region of Alamogordo is characterized by an average of 10.92 inches of rain annually and a mean temperature of 61 degrees F. (16.1 degrees C.). Vegetation is sparse and xerophytic. Both *Peromyscus* and *Perognathus* are found in the Desert Belts but *P. l. tornillo* is characteristic of the grassy washes which are believed to be the more favorable habitat of this belt. *Perognathus* ranges widely on the desert plains but is associated with *P. l. tornillo* in the grassy washes only occassionally. Southern Michigan in the region of Pinckney is characterized by an average annual rainfall of 31.35 inches with a mean annual temperature of 47 degrees F. (8.3 degrees C.). Vegetation is mesophytic with a number of hydrophytic forms. *P. l. noveboracen-*

sis is found chiefly, but not exclusively, in areas that are wooded or covered with heavy brush. Mice captured from the drier habitats evaporated significantly less moisture from lungs and skin than did mice captured from more mesic habitats.

Discussion

Insensible water loss is that which occurs through the skin and lungs. Under certain conditions this loss may serve to regulate body temperature, but under other conditions it is an unavoidable loss detrimental to the animal. Rodents have few or no sweat glands; however, a considerable amount of water is lost by evaporation from the skin. Physical factors affecting evaporation are temperature, humidity, and rate of air flow. Desert dwelling animals are adapted in several ways to minimize moisture losses.

The Schmidt-Nielsens (1950a) have shown that the humidity in an enclosed space 30 cm. beneath the surface of desert soil may reach 100% saturation and that surface humidities during the night are higher than during the day. It appears likely the burrowing and nocturnal habits of many desert animals are behavior modifications to conserve moisture. *Perognathus* is known to plug its burrow during the day. Howell and Gersh (1935) found the respiration rate of *Dipodomys* to decrease about one-half after seventeen days on a dry diet. Chew (1951) was unable to demonstrate a lower breathing rate in *Peromyscus* on reduced water ration, but did find metabolism 75% of normal. Lindeborg (1952) showed that several forms of mice were able to adjust to much reduced water ration. Several workers, Chew (1951), Schmidt-Nielsens and others (1948), Howell and Gersh (1935), and the author (unpublished) have demonstrated the ability of these forms to secrete a highly concentrated urine and also dry fecal pellets. Schmidt-Nielsens and others (1948) established that food selection may also be important because less water is needed to secrete metabolic wastes of a high carbohydrate diet. Reproductive adjustments are also suggested by Krogh's observations (1939), that seals and whales, which have very little fresh water available and are therefore living under "desert" conditions even though they are aquatic, secrete a highly concentrated milk. Lindeborg (1950) has suggested that breeding cycles are correlated with times of sufficient moisture availability. In all, it is apparent that a large number of physiologic and behavior adaptations and adjustments are essential for life in arid areas.

Summary

The measurements of water lost through evaporation by *Peromyscus* and *Perognathus* were made under experimental conditions more extreme than would be found under natural conditions. In completely dry air fourteen *Perognathus* evaporated an average of 0.80 cc. of water per day. Under the same conditions fourteen *Peromyscus l. tornillo* lost an average of 2.33 cc. per day. The difference, 1.52 cc. per day, is highly significant. Five female *P. l. noveboracensis* lost an average of 2.86 cc. per day or 0.53 cc. per day more than *P. l. tornillo*. Of the three races tested the ones that live in the drier habitats evaporate least water from lungs and skin.

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A NOTE ON GALLERY FORESTS

For reasons of space, a discussion of the interesting problem of the "gallery forests" which commonly follow the watercourses through savanna regions was withheld from the writer's paper on the savanna vegetation of northern tropical America (1953). It seems to be generally held that these forests are enabled to survive because of the supplementary moisture which they can derive from the presence of a watercourse, this "telluric" water supply providing more favorable moisture conditions than the savanna land away from the river. If the savannas were of climatic origin this would indeed be the logical explanation and does appear to apply to such forests in temperate grassland. However, it has been shown that the savanna in tropical America is of edaphic origin and does not simply represent a drier habitat (in terms of physical drought) than that of nearby forests. There must therefore be an alternative reason, associated with soil conditions, for the presence of gallery forests in the savanna.

Like all boundaries between savanna and forest, the borders of the gallery forests are abrupt, tall trees rising from the very edge of the grassland. As often as not the border is marked by a short but steep declivity from savanna level down to a riverain flat, but this is not a

necessary feature. Very rarely do the savanna fires penetrate and damage the gallery forest. Here and there on the Gran Sabana in Venezuela, the writer saw places where this had happened and the forest had been replaced by a slender bamboo.

The gallery forests are not a single type of vegetation but may consist of almost any woody formation. In the Venezuelan Guiana they vary from evergreen seasonal forest through semi-evergreen and deciduous seasonal forest down to thorn woodland. On the llanos north of the Orinoco, herbaceous swamp with Mauritia is usual on the lower courses of the tributary rivers but higher up it becomes deciduous seasonal forest or thorn woodland. South of the Orinoco along the Caura, Williams (1940) found extensive swamp forests. On the Gran Sabana, gallery forests belong to a somewhat specialized and reduced sclerophyll type, in the Brazilian savannas various kinds of seasonal forests are found and in the Chaco, palm swamp appears again. There is a very great diversity, but the gallery forests fall mainly in two groups, being either swamp or seasonal formations. The width of the gallery forest is also very variable and may range from a width of several miles down to complete absence along the banks of the same river.

Where the gallery forests are obviously swampy, composed of swamp forest or woodland, their ecological relationships are clear enough. The riverain flat is not high enough above water level to escape prolonged flooding and the vegetation is that associated with a normal high water table. It is those types where flooding is not a significant factor which provide more interesting material for study. In these cases, there is no correlation of width and luxuriance of the gallery forest with the breadth and permanence of the river, as we should expect from the telluric moisture theory. Some rivers are permanent, others dry up in the dry season, but this does not appear to affect the physiognomy of the forest on their banks. If the gallery forest were dependent upon supplies of telluric moisture in a dry region we should certainly expect the amount of moisture available from the river to be reflected in the life form of the forest.

One of the most significant facts about such gallery forests is that they seldom differ materially from other forests in the vicinity away from the river, on mountains, hills and other suitable forest sites. Where a very dry habitat occurs, like cavernous limestone *mogotes,* we may clearly expect its vegetation to be more xeromorphic than the gallery forest, and if the latter is subject to flooding, it will of course tend to differ from the upland forests. In most cases, however, there is a considerable degree of uniformity between gallery and upland forests. This is made clear in the Venezuelan Guiana where both the writer and Llewelyn Williams found the hill and the riverain forests (except for swamp types locally) to correspond and to vary with the rainfall of the district from evergreen to deciduous. In the Gran Sabana, the writer found no essential difference between the forests bordering the Kukenan River and those on the escarpments, both being of a specialized and sclerophyll type.

It is clear that gallery forests border the rivers wherever the peculiar soils of savannas with their perched water tables are replaced by soils of favorable drainage. Gallery forests, in fact, occupy belts of recent alluvia along the water courses, where the impeded drainage of savanna soils has not yet developed. These alluvial soils are porous and well-drained with a normal water table. This explains the varying width of the gallery forest, since young alluvial flats will not be of constant extent. In traveling on the Guiana highlands, Schomburgk (1847) made it clear that the exposed soil in riverbanks was deep and permeable under forests, but that when the savannas came down to the water's edge their subsoil was seen to consist of ferruginous conglomerate.

Gallery forests, where they are not on swampy sites, represent the climatic climax of the region. This explains their correspondence with upland forests and the variation of both from place to place with changes in rainfall.

These conclusions may not be found to apply in savanna country in tropical Africa, so much of which is due to the destruction or opening of forest by fire. Gallery forests in fire grassland may have resisted burning due to greater luxuriance derived from telluric moisture.

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PHOTOPERIODISM AND THE DEVELOPMENT OF *AEDES TRISERIATUS* (DIPTERA: CULICIDAE)

A laboratory colony of *Aedes triseriatus* has been maintained at the Newton, Georgia, Field Station to supply material for studies on the transmission of malaria and filaria infections of lower animals. This colony was established and is maintained as described by Repass (1952). Normally, development from ova to adults required about 15 days. During the fall of 1951, it was noted that the number of pupae being obtained was far below normal and that many larvae on the shelves of the insectary rearing room were 6 weeks to 2 months old. These larvae appeared to be healthy, exhibited a characteristic negative phototropism, apparently fed normally, and, in general, appeared no different than larvae obtained at other times of the year.

Baker (1935), reporting on various tree-hole species in the vicinity of Ithaca, New York, stated that *Orthopodomyia signifera, Orthopodomyia alba,* and *Culicoides guttipennis* overwintered as larvae and pupated in the spring after the photoperiod was lengthened. He concluded, however, that *Ae. triseriatus* in that area over-

wintered as photosensitive ova which hatched during the longer days of spring.

Although increased crepuscular activity, such as the swarming and feeding, of many species of mosquitoes has frequently been observed, very little has been done on the relation of photoperiodism to mosquito development in this country. In January of 1952, a study was initiated to determine the relation of the photoperiod to the development of *Ae. triseriatus* in southwestern Georgia.

Material and Methods

All ova and larvae used in the study were taken from the self-perpetuating colony of *Ae. triseriatus* maintained in the insectary. Similarity of reactions in natural material was checked with specimens obtained from four tree-hole collections. Ova were collected on small oak blocks 1 x 1 x 3 inches and dried slowly for a period of 10 days. They were then flooded with well water. Larvae were reared in enamel pans approximatetly 8 x 15 x 2 inches. Water was maintained in the pans at a depth of approximately 1½ inches. Larvae were fed powdered dog biscuits once each day.

For study purposes, fourth instar larvae in lots of 25 each were placed in biological specimen bowls 3 inches in diameter and exposed to the various conditions. At least two replicate series were used in each instance. First instar larvae were used in lots of 10 each and placed in 1-ounce square bottles which could easily be placed in the light boxes designed for the study. Five replicates were always used in the boxes.

Artificial light was supplied to fourth instar larvae or adults by placing a 100-watt bulb approximately one foot above the bowls or cages containing the study material. Water temperatures in the bowls were checked daily. Heat generated by the light maintained the temperature of the water at approximately 3° C. above room temperatures. Constant high or low water temperatures were maintained with a controlled temperature water bath.

Exact length of the photoperiod was controlled with boxes approximately 2 feet tall and 6 inches square. For ventilation, two light-tight baffles were placed in the boxes, one 2 inches from the bottom and one 12 inches from the bottom. A 15-watt bulb was attached to the removable top of the box. Larvae were placed in the bottom of the box with a thermometer from which daily temperature readings were made. Temperatures in the bottom of the boxes were never more than one degree above the room temperature.

In all, a total of 1,000 larvae were studied under various conditions of temperature and light in addition to the control specimens used for each segment of the study.

Results and Discussion

No indication of light affecting the hatching of the ova was obtained. Ova collected from the colony cage on the morning after oviposition and allowed to dry slowly, either in complete darkness or in constant light, hatched readily when submersed in water.

To determine the factors responsible for decreased pupation in the fall of the year, two replicate series of fourth instar larvae were placed under a constant light in a room where heat was maintained at 26.7 degrees C. Water temperature in this series was approximately 29 degrees. Two series were placed in complete darkness at approximately 27 degrees. Two series were placed in a 7-degree water bath with natural winter light fluctuations, and two series placed in a 39-degree water bath with natural winter light variations. A number of series were placed on a shelf in the insectary for controls. Results of this test are shown in Table I.

Table I. *Effect of constant light, complete darkness, and high and low temperatures on the pupation of fourth instar "winter"* Ae. triseriatus *larvae*

Conditions	Results
1. Controls - Natural winter light variations. Constant 27 degree temperature.	(a) No pupation after 40 days.
2. Constant darkness and 27 degree temperature.	(a) No pupation after 40 days.
3. Natural winter light variations. Constant 7 degree temperature.	(a) No pupation after 16 days.
4. Constant light and 7 degree temperature.	(a) After 16 days under condition 3 (above) larvae were placed under condition 4. No pupation occurred after 24 additional days.
5. Natural winter light variations. Constant 39 degree temperature.	(a) Larvae survived for 14 days. No pupation occurred.
6. Constant light and 29 degree temperature.	(a) First pupa obtained 4 days after exposure. Pupation was complete after 9 days. (b) After 9 days at condition 1 (above) larvae were placed under condition 6. Pupation began after 4 days and was complete in 9 days. (c) After 9 days at condition 2 (above) larvae were placed under condition 6. Pupation began in 4 days and was complete in 9 days. (d) After 30 days at condition 1 (above) larvae were placed under condition 6. Pupation began in 4 days and was complete in 9 days. (e) After 16 days at condition 3 and an additional 14 days at condition 4 (above) larvae were placed under condition 6. Pupation began in 4 days and was complete in 9 days.

Within 5 to 9 days, all larvae under the constant light and at room temperature had pupated, but no development was apparent under the other conditions. One series of larvae was then removed from complete darkness and room temperature and placed under the constant light at room temperature with one of the control series from the insectary. These also all pupated 5 to 9 days after removal to constant light conditions. A continuous light was then placed over the larvae at 7 degrees for 2 weeks, but no development was noticed. One of these was removed from the reduced temperature and placed with one control series under the constant light at 29 degrees. Again all of these larvae pupated 5 to 9 days after being placed under the new conditions. Apparently the lengthened photoperiod at 7 degrees did not stimulate development, even at a reduced rate, since the rates of pupation for the series removed from 7 degrees and for the control series paralleled one another so closely. Larvae placed at 39 degrees survived for approximately 2 weeks without development.

Four January collections of wild *Ae. triseriatus* larvae from tree-holes in the area were brought into the laboratory and placed under constant light at room temperature. The larvae from these collections also pupated on the same schedule as was found for the colonized specimens.

After the natural photoperiod became sufficiently long to permit normal continuous development in the insectary

colony, studies were begun to determine the lengths of photoperiods necessary for the development or retarding of development of *Ae. triseriatus* larvae. By observation of the laboratory colony for two years a photoperiod of approximately 13 hours was determined empirically as necessary for continuous development and investigations were designed to substantiate these observations. Newly hatched first instar larvae were placed in light boxes and exposed to photoperiods of 15, 13, 9, 7, and 2 hours. Others were kept in complete darkness. In every instance, larvae developed and pupae were obtained in the same number of days that pupae were obtained from control series exposed to the natural July light fluctuations.

Since it was obvious that larvae reared during the winter months when the days were short pupated only when the photoperiod was lengthened, and that ova obtained during the summer months when the days were longer gave rise to larvae which would develop in complete darkness, it was concluded that the shortening of the days with the approach of winter must result in the production of a different type of ovum. Only these winter-type ova produced larvae which respond to variations of the photoperiod.

When the natural photoperiod again became short enough to retard the production of pupae in the laboratory colony, tests were run to determine the effect of an extended light period on the ovipositing females. If the conclusions regarding ova were correct, the progeny of these females should develop in complete darkness. Artificial light was supplied for approximately four additional hours in the morning, thus not interfering with the natural evening crepuscular period during which mating and oviposition probably occur. Ova obtained were dried under natural light variations and later flooded and placed in complete darkness. The results obtained from these tests were not entirely conclusive. Most of the larvae obtained for 2 weeks after supplemental light was added developed and pupated in complete darkness. Some apparently did not. Due to irregular observations, however, it was impossible to tell if all the ova hatched at one time, or if some or all of the larvae remaining in the pans resulted from a delayed hatching of some of the ova. These larvae were observed for only 20 days, at which time some larvae still remained.

The following summer, when larvae were again pupating normally, a cage of adults was placed in a darkened room for a period of 2 weeks, and then ova were collected. On the same day ova were collected also from the colony cage exposed to natural light fluctuations. Ten days later both lots of ova were flooded and placed in rearing pans in the darkened room. Larvae obtained from colony-cage ova developed and pupated normally. Most of the larvae obtained from dark-room ova developed to the fourth instar, but did not pupate until the photoperiod was lengthened. Here again, however, the results were not absolute since a few of these larvae did pupate. These discrepancies in the results obtained are very likely due to variations in the intensity of stimulation needed to affect individual specimens.

These studies indicate that *Ae. triseriatus*, at least in southwestern Georgia, overwinter as larvae in the same manner that Baker reported for other tree-hole species of mosquitoes and *Culicoides*. There has been no indication of *Ae. triseriatus* ova being affected by light as described by Baker for the Ithaca, New York, area.

Summary

Studies were made on the effect of the photoperiod length on the development of *Ae. triseriatus*. Ova hatched normally after being maintained either in constant light or complete darkness. In the insectary colony, pupation was retarded as the natural photoperiod was shortened in the winter months. These larvae pupated readily when stimulated by a longer period of light at a moderate temperature. An extended photoperiod did not effect pupation at 7 degrees C. Larvae obtained in midsummer developed and pupated in complete darkness. Adult females exposed to approximately 15 hours of light in midwinter produced progeny which developed and pupated in complete darkness. Ova obtained in midsummer from a cage of adults in a darkened room produced progeny which would not pupate until the photoperiod had been lengthened. It is concluded that shortening the photoperiod in the fall provides the stimulus which results in the production of a characteristic winter type of ova. Only larvae hatched from these ova are affected by variations in the photoperiod.

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ESTIMATION OF THE NUMBER OF SPECIES PRESENT ON A GIVEN AREA

A reliable estimate of the number of species to be expected on a given area has practical as well as theoretical importance. In survey work, for example, it would be useful to have some idea as to whether or not a satisfactory proportion of the species had been collected. It has long been observed that, in sampling the flora or fauna of a given area, if one takes a series of samples so as to include a progressively larger portion of the area and records the number of species encountered, a plot of the number of species against the size of the sample yields a curve whose slope is relatively steep at first but which tends to flatten out as one moves to the right. This relationship was first studied by plant ecologists, who took samples of increasing area, and the curve has therefore become known as the species-area curve, but it is of course equally applicable to samples of increasing volume or of increasing distance. If, as was pointed out by Gleason (1922), the number of species is plotted against the logarithm of sample size rather than against the actual size, the species-area curve will be represented as an approximately straight line, at least through the region of the observations. This species-area

line can then be used to predict the number of species to be found in an area of specified size. For this purpose, the relationship may conveniently be represented by the following formula:

$$S = \frac{s}{\log (n+1)} \log (N+1)$$

where S is an estimate of the number of species expected on an area consisting of N units and s is the number of species encountered in n units selected at random. The transformation using the logarithm of n + 1 causes the species-area line to pass through the intersection of the coordinates and thus permits a better estimate of S when this is based on relatively few samples.

Various attempts have been made to estimate by this means the number of species expected on given areas, but it has generally been impossible to test the reliability of these estimates because complete lists of species known to be present were not available for comparison. Recently we had an opportunity to make such a test. A 15-acre abandoned field on the E. S. George Reserve at Pinckney, Michigan, has been subjected to intensive ecological study for the past six years, and 130 species of vascular plants have been discovered on it. The floristic composition of this field is quite stable, and it is believed that this number of species closely approximates the total number present on July 1, 1953, when species-area data were collected on 54,000 square yards of this field by taking a series of 200 randomly selected square-yard samples and by recording species occurrence in each sample. The samples were recorded in the order of being drawn, and since there were no duplications it was possible to consider them in sets of various sizes, each set being independent of any other set of the same size. The numbers of species encountered in these sets of samples and the estimated numbers of species derived from these observations are given in Table I. The entire series of 200 samples represents only 0.37 per cent of the total sample area, yet it recorded 63 species, or almost half of the number of species known for the whole field. The estimated number of species based on the entire series of samples is 129.5, an extraordinarily close fit to the known number of 130 species. Another set of 200 samples would undoubtedly have yielded a slightly different estimate. Some idea of the variation to be expected in such estimates can be obtained by considering those based on successive sets of different sizes, as shown in Table I. Although the various estimates differ among themselves, almost all of them are of the right order of magnitude.

TABLE I. *Estimates of the number of species of vascular plants occurring on a 54,000 sq. yd. area of an abandoned field on the E. S. George Reserve, Pinckney, Michigan, based on the numbers of species encountered in sets of sq. yd. samples taken at random*

Number of samples in set	Number of species encountered in sampling	Estimated number of species on total area sampled
25	46	153.8
	42	140.5
	38	127.1
	42	140.5
	42	140.5
	39	130.4
	40	133.8
	38	127.1
50	54	149.7
	49	135.8
	47	130.3
	46	127.5
100	59	139.3
	51	120.4
200	63	129.5

In using such a procedure to estimate the number of species, it is of course important to avoid extrapolating beyond the limits of the area from which the samples were taken. It is also important to expose to sampling the entire area for which the estimate is desired and to take the samples in as random a manner as possible. The example given above suggests that, if these precautionary measures are followed, a satisfactory estimate of the number of species can be obtained.

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THE EASTERN LIMIT OF THE SONORAN DESERT IN THE UNITED STATES WITH ADDITIONS TO THE KNOWN HERPETOFAUNA OF NEW MEXICO[1]

In the latest and most detailed analysis and classification of the Sonoran Desert, Shreve (1951) again maps the eastern limit of this major ecologic formation, in the vicinity of the Mexican boundary, wholly within the limits of what is now the state of Arizona, and not so far east as Safford, Graham County. This conclusion has merit. It is defensible as an interpretation involving the vegetational characteristics of what is essentially an area of Desert-Grassland ecotone between the Sonoran Desert to the west (in southern Arizona) and the Chihuahuan Desert to the east (in southern New Mexico).

However, the matter of the eastern limit of the Sonoran Desert in this region remains one of interpretation of both long-standing and more recently acquired distributional facts for both plants and animals. Thus one may consider the Sonoran Desert limit in question as one of the three following: (1) as presented by Shreve (*op. cit.*), (2) as extending eastward into extreme southwestern New Mexico, along the drainages of the Gila River and San Simon Creek (see Benson and

[1] Charles M. Bogert of the American Museum of Natural History collected the majority of the New Mexican lizards reported on herein, read the manuscript, and made valuable suggestions which have been incorporated.

Darrow, 1944: 10, map), or (3) as extending eastward into extreme southwestern New Mexico somewhat beyond the immediate drainageways of the Gila and San Simon.

Animal distribution is in accord with the general conclusion of Benson and Darrow, as opposed to that of Shreve, as to the eastern limit of the Sonoran Desert at this latitude. In fact, concordance of the distribution of both cold-blooded and warm-blooded vertebrates with the mappable reality of this region of the Sonoran Desert as shown by Benson and Darrow for plants, is such that a respectable degree of predictability obtains as to the occurrence of certain Sonoran Desert animal genera, species, and subspecies in extreme southwestern New Mexico. The recently verified present occurrence of the Gila Monster (*Heloderma suspectum*) and Sonoran Coral Snake (*Micruroides euryxanthus*) in southwestern New Mexico, as also discussed below, are more than usually interesting cases in point.

During field work with Charles M. Bogert, in July 1953, the known ranges of two genera of desert lizards, *Callisaurus* (diurnal) and *Coleonyx* (nocturnal), were extended eastward from southern Arizona into southwestern New Mexico. These were taken in the San Simon drainage in Hidalgo County, New Mexico, at the following localities:

Callisaurus draconoides ventralis (Hallowell)
17.5 miles NNE Rodeo, Hidalgo County, New Mexico. Several.
Coleonyx variegatus bogerti Klauber
Granite Gap, ca. 20 miles NNE Rodeo, Hidalgo County, New Mexico.[2] Three.

The *Coleonyx* and some of the *Callisaurus* are deposited in the American Museum of Natural History; some of the *Callisaurus,* in the Department of Zoology, University of Arizona. A specimen of *Callisaurus d. ventralis* was collected by C. M. Bogert in August 1953 on the Arizona side of the state line in San Simon Valley, at the Alden Hayes Ranch, northeast of Portal, Cochise County. We collected several additional specimens in the San Simon drainage at 8.2 miles (by rd.) east of San Simon, ca. 3900 ft., Cochise County, Arizona.

These new distributional records for vertebrates of the Sonoran Desert lend further important emphasis to a conclusion that animal distribution in general is consistent with an interpretation of the extreme eastern limit of the Sonoran Desert in the United States as resting today in extreme southwestern New Mexico. Thus the eastern limit is at least approximately confluent with the immediate drainages of San Simon Creek and the Gila River in this area, approximately as mapped by Benson and Darrow (*op. cit.*). The Peloncillo Mountains of Hidalgo County, New Mexico, form the extreme eastward watershed of the San Simon Valley.

Both the Gila River and San Simon Creek are in the Colorado River basin and have their origin in southwestern New Mexico. Each is in southern Arizona for the greater part of its total extent. As these drainages course westward from New Mexico into Arizona, they became progressively lower in elevation and accordingly become progressively more characterized as Sonoran Desert environments. As conversely considered, the biota of the Sonoran Desert fingers eastward up these major channels from southern Arizona into the southwestern corner of New Mexico.

Primarily on the basis of plant and mammal distribution, Mearns delimited at approximately the Arizona-New Mexico state line an "Eastern Desert Tract" in southern New Mexico and an "Elevated Central Tract" in southeastern Arizona. He depicted the latter "Tract" as extending into New Mexico along the Gila River. Thus Mearns also considered what is now termed the Sonoran Desert (Shreve 1942) as extending into the southwestern corner of New Mexico.

Primarily on the basis of bird distribution, Phillips (1953) has recently suggested that the eastern limit of the Sonoran fauna (but not the fauna of the Sonoran Desert proper) may be tentatively construed as approximated by a north-south line between the Animas Range and the Big Hatchet Mountains of Hidalgo County, New Mexico, and extending a short distance northward and southward; northward into extreme southern Catron County, including Silver City (Grant County), New Mexico, and southward into the extreme northwest corner of Chihuahua, Mexico, inclusive of the Sierra San Luis but exclusive of virtually all of Chihuahua. With regard to the avifauna of the Sonora Desert Proper, Dr. Phillips informs me that *its* eastern limit is in the vicinity of the Peloncillo Mountains of Hidalgo County, New Mexico, which mountain range lies just to the west of the Animas Range.

The matter of such a boundary as that of a desert is, in final analysis, an academic one, and there should be no particular expectancy for fundamentally different animal types to show more than general concordance in those east-west distributional limits as reached for example in extreme southwestern New Mexico. Therefore, it is of more than usual interest that from independent analysis of the distribution of warm-blooded vertebrates, cold-blooded vertebrates, and of plants, it has been concluded by various authors that the general region of the Peloncillo Mountains in Hidalgo County, New Mexico, approximates today the eastern limit of the Sonoran Desert at this particular latitude.

The map in Benson and Darrow (*op. cit.*) shows the Sonoran Desert extending eastward in the drainage of the Gila River to approximately central Grant County, New Mexico. In concordance, the Gila Monster (*Heloderma suspectum*) and Sonoran Coral Snake (*Micruroides euryxanthus*) both occur in this region. Woodson's data (in Shaw 1950) recording Gila Monsters in the vicinity of Redrock (southwest of Silver City), and Woodin's (1953) report of a specimen of the Sonoran Coral Snake taken at 11 miles northeast of Cliff, establish the logical occurrence of these Sonoran Desert reptiles along the Gila River drainage in Grant County, New Mexico. Both the Gila Monster and Sonoran Coral Snake are characteristic vertebrates of the eastern section of the Sonoran Desert along the Mexican boundary. From the data presented by Shaw (*op. cit.*) it is clear that the range of the Gila Monster extends in Hidalgo County to the Peloncillo Mountains and adjacent edge of the Animas Valley (Granite Gap, Steins-Road Forks), and may also occur in the Pyramid Mountains just to the northeast of the Peloncillo Mountains. All of this area is just to the west of the Continental Divide.

Little is known concerning the ecological distribution of lizards in the Animas Valley to the east of the Peloncillo Mountains. The recent collection of *Sceloporus poinsetti* from a small outcrop of volcanic rock not far north of the town of Animas, by C. M. Bogert in 1953 (*in litt.*), constitutes an important eastward extension

[2] The Gila Monster (*Heloderma suspectum*) is also recorded from Granite Gap, as observed (DOR) on May 14, 1945, by Paul E. Hudson, County Extension Agent, Lordsburg, New Mexico (Woodson, in Shaw 1950).

of the known range of this species. The question remains as to its occurrence in the Peloncillo Mountains to the immediate westward, where it has been sought but not found. This species is not known from the Colorado River basin and probably does not occur there. From its disjunctive range in extreme western New Mexico it extends eastward into Texas and southward into Mexico.

The ecological distribution of lizards in San Simon Valley, which is to the west of the Peloncillo Mountains, is particularly spotty. Here local populations of such conspicuous forms as *Callisaurus draconoides, Cnemidophorus tigris, Sceloporus undulatus* and *Cnemidophorus inornatus* are obviously correlated to some extent with local environmental variations of physiography and/or vegetation type. For example, *Callisaurus* and *Cnemidophorus tigris* appear to occur here predominantly or excusively in local communities dominated by Creosote bush (*Larrea tridentata*) as opposed to those dominated by Blackbrush (*Flourensia cernua*) or *Yucca*-grass. An inviting ecological and evolutionary study of the relationships of the fauna of a Desert-Grassland ecotone is presented in this area. This general region presents a complex confluence of Grassland, Sonoran Desert, and Chihuahuan Desert biotas.

In summary, (1) the known distributions of genera, species, and subspecies of the herpetofauna of the Sonoran Desert concord with the interpretation of Benson and Darrow (1944) rather than that of Shreve (1951) as to the eastern limit of the Sonoran Desert in the United States; (2) the Sonoran Desert ecologic formation extends into Hidalgo and Grant counties, New Mexico, in the drainages of the Gila River and San Simon Creek, and its extreme eastern limit at this latitude is approximated by the immediate western alluvia of the Burro Mountains, Pyramid Mountains, and southern Peloncillo Mountains; (3) in the general vicinity of this limit, the biota of the Sonoran Desert is in complex ecotone with more eastern biotas; (4) the eastern limit of the Sonoran Desert in the United States as thus interpreted is in the approximate position of the eastern limit of the Colorado River basin at this latitude.

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A SPRUCE-FIR STAND IN THE NORTHERN PENINSULA OF MICHIGAN

This note records a small stand of spruce-fir in the northern peninsula of Michigan. Stands of boreal forest in this area are infrequent and therefore noteworthy.

A very small, isolated stand of *Picea glauca-Abies balsamea* is located along a creek on the estate of Mr. Guido Rahr, 46° 10′ N 89° 25′ W, Gogebic County, Michigan. The area has been protected from cutting by the owner, and to some extent from fire by swamplands which surround it. During the summer of 1954, the composition of the tree layer (4 inches DBH or over) was studied by a modification of the random pairs method. In the modified method, five trees were recorded at each of twenty random points. Relative frequency is the expression of the frequency of each species as a per cent of the sum of frequency of all species. Results appear in the accompanying table. (Table I).

Table I. *Tree data for spruce-fir stand in the Northern Peninsula of Michigan*

Species	Relative frequency (%)	Relative basal Area (%)	Density per 100 trees
Abies balsamea (L.) Mill.	28	18	31
Acer rubrum L.	2	1	1
Betula lutea Michx.	3	2	2
Betula papyrifera Marsh.	16	14	10
Larix laricina (DuRoi) K. Koch	5	3	3
Picea glauca (Moench) Voss.	29	51	42
Picea mariana (Mill.) BSP.	10	4	6
Thuja occidentalis L.	7	7	5

The largest tree of *Picea glauca* had a basal area of 115 sq. in., and the approximate average basal area for spruce was 60 sq. in. The largest specimen of *Abies balsamea* had a basal area of only 55 sq. in., and the approximate average basal area for fir was 28 sq. in. Average distance between individuals of the stand was about 13 feet, or approximately 258 trees per acre.

Herb data are not presented since a beaver dam downstream had recently backed up the water over the low streambanks and no doubt had affected the ground layer. Carices were abundant, including *Carex disperma* Dew., *C. trisperma* Dew., *C. stricta* Lam., *C. intumescens* Rudge, and *C. leptalea* Wahlenb. Indicators of the boreal forest present included *Trientalis borealis* Raf., *Viola pallens* (Banks) Brainerd, *Clintonia borealis* (Ait.) Raf., *Coptis groenlandica* (Oeder) Fern., *Cornus canadensis* L., and *Maianthemum canadense* Desf.

The soil was waterlogged, a condition probably due to the beaver dam and not typical of a spruce-fir forest. One boring disclosed sand at 1 foot depth; other borings showed peat to a depth of at least 3 feet.

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NOTES ON A LEAF-ROLLING CATERPILLAR AND ON SOME OF ITS ASSOCIATES

There is a curious assemblage of insects to be found on the false nettle, *Boehmeria cylindrica*. I studied it in Florida during the winters of 1951-52-53 at the Archbold Biological Station near Lake Placid. This study began when I unexpectedly came upon a multitude of leaf-rolls on this common ditch-side weed—beautifully cylindric rolls in all stages of construction and demolition. Here was an opportunity to study the leaf-rolling habit; to see how a little moth larva makes for itself a dwelling place, rolling up a single leaf, fastening the layers in place by means of silken cords and living in it until time for its transformation to a winged adult moth.

First, a few words about the false nettle that is the all-essential part of the environment for several of the species here discussed, that provides food or shelter for all of them. It is a nettle-like weed (family Urticaceae), so nearly destitute of stinging hair that it may be handled without discomfort. It grows in small clumps on perennial, creeping rootstocks, and rises on erect stems to heights of a meter or more on moist soil and in partial shade. Though well scattered along the sides of the Station ditch, one large clump (about two square meters) very near the laboratory, furnished most of the material for this paper.

The long-stalked leaf blades are generally from three to five inches in length, broadly lanceolate in outline, pointed at the tip, rounded at the base, and with coarsely serrate margins. Their color is bright green above, pale beneath. Their texture is soft, their surfaces nearly hairless and their main veins prominent on the under side.

Opening a few of the rolled-up cylinders quickly yielded both larvae and pupae of a little moth that lives inside them. I soon reared the adult moth and sent specimens of it to the U.S. National Museum where Mr. Hahn W. Capps determined it for me and reported that nothing was known of its life history and habits.

Sylepta and Its Associates

Sylepta silicalis (Guen.)

This moth is of the ordinary pyralid form. Its wings are folded roof-like over its back and have a spread of about 32 mm. It is nearly monochrome pale brown in coloration. The front of the body is heaped with a deep layer of extremely long, shining, straw-colored scales that overspread the thorax like a shawl. The wings are of a little darker tint and are crossed toward their outer margin by three faint, narrow, parallel wavy bands of brown.

I have never seen this moth alive in the field, though several times I have taken a lighted lantern out among the clumps of Boehmeria in search of it. The light did not attract them, and none came to the nearby lights of the field station not a hundred meters distant.

The larva when grown is about 15 mm. long and 2 mm. in diameter. It is cylindric, glassy green in color and so translucent that the stomach, which occupies most of its length, is readily seen from the outside. It is generally crammed with dark green freshly ingested browse. The skin of the body looks naked in life until one looks more carefully and sees that it is thinly beset with long transparent hairs; some of them as long as the diameter of the body. Head and thorax are patterned in brown, pale beneath. An uneven pale middorsal line divides the brown on the disc of the prothorax; on the head, however, the brown is broken up into patches that give it a freckled appearance; on top these sometimes form a distinct pattern like this—) (. Behind the five whitish eyes the bulging hind angles are dark brown. The prominent mandibles also are brown.

The larva is exceedingly active, runs forward and backward equally well in its roll, and when fully uncovered, flings itself about in most violent contortions. If too much disturbed it may leap for safety, sometimes falling to the ground, sometimes swinging out and down on a silken thread, as does the better-known green canker-worm.

In order to see how a roll is made I unrolled and flattened out a half-completed one. I first cut the binding cords that hold the layers in place, and took out the larva. I then lifted out the frass pellets that are hung up separately on silken threads, and I carefully wiped out the silk tangle already spun. Then placing the inverted leafblade on a sheet of paper, I placed the larva on it.

On the bare leaf the larva crept about with far less speed than on its former thread-tangle, though with greater effort. For a time it sought to creep off the leaf, and I kept barring its exit at the leaf margin. A touch on its skin anywhere would make it change its course. After a time it stopped and rested a bit and then began an obvious exploration of the leaf surface.

Then it explored the margin and finding one marginal tooth a little higher than the neighboring ones, attached a spot of silk to the tip of it, and drew out a shiny thread, excessively slender, just visible in a good light, with round globules of fluid silk ranged along the thread as on a string of widely spaced beads. It then reached as far as it possibly could in the opposite direction and attached the other end of this thread to the under surface of the leaf. I could see the tooth on the leaf margin lifted a little by the pull of this thread. Then holding fast with all its prolegs, its thoracic legs hanging free, it swung back and forth laying additional treads alongside that first one. And so it continued for perhaps a minute swaying back and forth as it added more threads. It made about three cross trips a second. Meanwhile I could see the lateral tooth of the leaf margin rising and pulling other teeth upward with it. Thus the roll was begun.

Then the larva backed up a little and proceeded in like manner to lay other cross lines of single threads, from nearby teeth on the leaf margin, parallel to the first one, and in a few minutes the upcurving margin was turning inward above the larva's back (Fig. 1).

At times I could see that the forelegs of the larva were being used to hold the issuing silk thread close against those already laid down, aiding the fusion of the threads into a single cord.

Soon further spinning was hidden from view beneath the uprolling leaf margin; but I could see that slender diagonal lines of silk were being spun in various directions and that the larva was no longer standing on the leaf surface but on these added lines.

Desiring to see more of the plan followed by the larva in laying down the interior lines of silk, I put a naked larva in a glass tube that had about the same diameter as a leaf roll. I plugged the ends with cotton, laid a green leaf over it for shade, and left it overnight. The next morning I could find no plan in the spinning done. But few lines had been laid down on the surface of the glass. From these ran a tangle of diagonal threads, with somewhat more of them toward the lower side of the tube. Soon I come to see the acrobatic larva as a kind

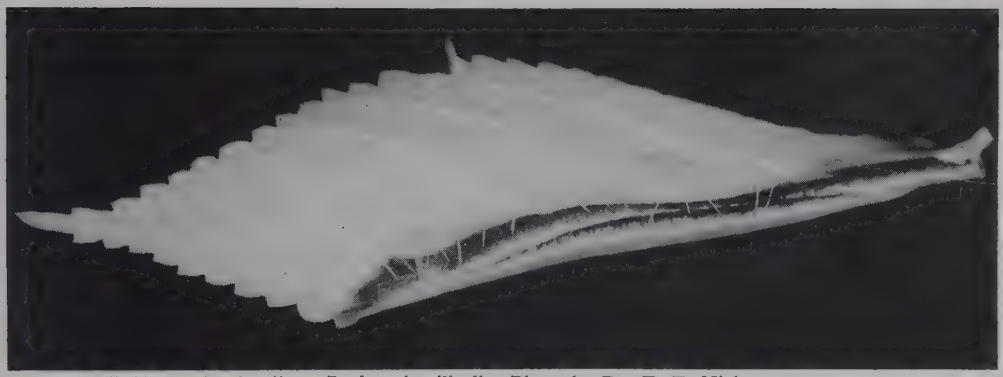

FIG. 1. Half completed roll on *Boehmeria silicalis*. Photo by Dr. E. T. Nielsen.

of trapeze performer, making its swiftest movements with complete skill and abandon, grasping and freeing the lines of silk with the crotchets of his amazing prop legs.

Another larva I kept in a bare glass tube and gave no food for more than twenty-four hours. Then I placed it on the under side of a fresh leaf, expecting to see it eat greedily. Instead, as soon as it came to rest on the leaf, it began exploring the surface, then found a suitable margin and began a leaf roll just as described above, and did not stop to eat until the roll was completed. "Safety first" was expressed in this; feeding did not begin until shelter had been made ready. Opening this roll again the next day I found that the larva had fed for a time on the folded edge of the leaf within the tubes, removing a strip of the innermost leaf margin parallel with the axis of the roll. Eating from that margin always stops while there is left plenty of overlap for safety.

The sanitation methods of this leaf-roll resident interested me greatly. Food residue and bodily wastes are gathered up into more or less cubical pellets of "frass" as with other leaf-eating moth larvae; but this larva hung up each pellet on a short silk thread of its own, attached to the inner wall of the roll where it dangled in the freely circulating air, and dried so quickly there was not time for fermentation or decay. Thus the walls and the ceiling of the larva's living room are decorated with harmless and inoffensive dots of black. That these pellets swing freely from the walls may be easily demonstrated by confining a young living larva in a bare glass tube over night, and in the morning watching the pellets swing while rotating the tube.

Each Sylepta larva makes several rolls, each roll above the one abandoned on the same stem. It occupies them in succession, thus it shifts toward ever fresher forage. The lowermost roll, when there are several, is always tattered and obviously abandoned; only the uppermost may contain a still-active larva or a pupa. Until time for pupation each roll is open at both ends—a free runway for the restless larvae, and a possible way of escape from invading pursuers.

A typical leaf roll involves about two-and-a-half layers of the leaf blade. The outermost layer is stitched down by 10-12 cords of silk; each splay-footed cord is composed of 25 to 50 separate threads, and is so strong that if lifted, the leaf will tear before the cord will break.

If one opens the roll of a half grown larva by carefully cutting its silk fastenings, spreading apart the freed layers and then peeping in, a larva may be seen resting in the air on the silken cords of its trapeze, so to speak, not down on the leaf surface; but quite free to move in any direction.

When the larvae are nearly grown they do much feeding by reaching outside the roll—probably at night when its diurnally active Bassus parasite is not abroad. Often the long acuminate apex of the leaf is entirely eaten away. Generally in large leaves when the basal half of the roll is abandoned, the part beyond becomes its final place of residence. Often so much is eaten that the occupied outer end of the leaf blade bends downward.

A larva may be kept in a handmade cylinder made by rolling a fresh leaf around a penholder and fastening the roll with a fine pin or needle stitched into its wall lengthwise. If offered no other shelter it will enter this and will feed on the ends of the roll. I kept a larva thus for about a week by supplying it with a fresh leaf roll every day.

I put a grown larva in such a short handmade roll with several fresh leaves laid alongside. It stayed in my roll, ate all the leaves and ejected large quantities of frass. Seeing that it had partly finished its pupation endsheets, I put it in a new short roll without added leaves, and it went on from that point in its preparatory work and pupated.

There is no cocoon spun by this moth larva. Preparatory to transformation, silk is spun toward the ends of the roll to make a pupation chamber. I have not traced the steps in detail but the main features of it seem to be about as follows: After the heavy feeding of the last larval instar, the abundant frass then produced is massed at two distant places in the roll and covered with freshly spun silk. Additional silk is spun to form two end sheets for a pupal chamber, a little farther apart than the length of the grown larva. Each end sheet is composed of many silken threads which cross at the center, greatly thickening it there. The inner surface of each end sheet is concave. There is no continuous lining of silk to the walls of the chamber; it is not cocoon-like at all.

Within this chamber, after the end of spinning, the larva changes in appearance. It becomes whitish, and opaque. These changes are, of course, the signs of the metamorphosis that is going on inside it, reshaping it to form the pupa. Its skin becomes broken by internal pressure at the front with the usual cracking of the hard head capsule for release. Another break at the rear permits attachment of the pupa's cremaster hooks to the middle of the end sheet.

The leaf rolling habit is not very rigidly fixed in this species. The roll may be begun at either right or left

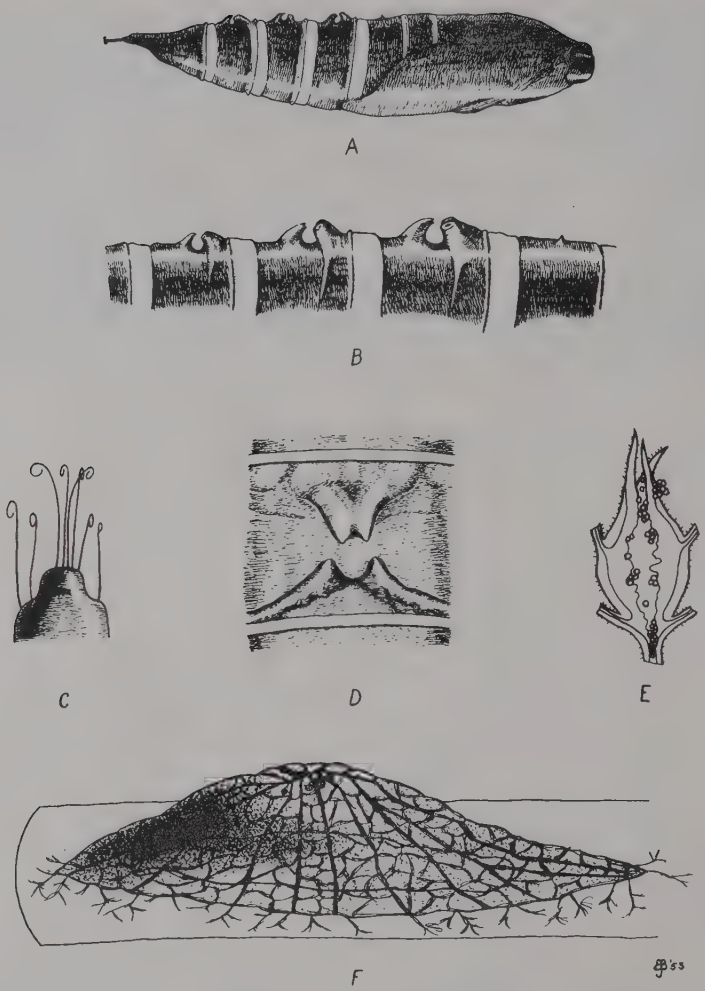

FIG. 2. A, B, C, and D—*Sylepta silicalis*. A—Pupa. B—Profile view of dorsal tubercles. C.—Caudal hooks. D—Dorsal view of tubercles. E—Gall on *Bohemeria cylindrica*, caused by larva of Machlotica. F—Pupal shelter of Machlotica.

margin of the leaf, or from both sides at once, in which case there is not material enough to complete either. Sometimes a leaf-tie is made between two leaves that chance to lie in contact; but this I have found only at the top of several successively occupied rolls. The two concave end sheets complete a clean pupation chamber between them.

An active larva, removed from its roll and given only small pieces of fresh leaves, will make a tubular cover for itself out of the pieces, like any ordinary leaf tyer; and if kept supplied with fresh pieces, will finally make endsheets in it and pupate as in a leaf roll, using its scanty remaining supply of silk to build a sheet at one end for attachment of the cremaster—a necessary preliminary for removal of the loosened larval skin. Clearly, what it will do is conditioned by what silk it has left to do with.

This end-sheet-building habit, however, seems to be less firmly fixed. A whitening opaque and evidently full fed larva, placed in a handmade roll of white writing paper and kept in the dark, made end sheets, as in leaf rolls. Another full-fed larva given only a creased sheet of writing paper, cut a notch in the edge of the paper, pulled in a flap for cover and spun an end sheet across it. Another placed in a bare laboratory slide-staining dish with vertical grooves at the ends, and given no cover at all but kept in the dark, attempted to form an end sheet across the bottom of one of the vertical grooves. Apparently the activity normal to the stage of physical development is fixed and it will use whatever material the environment affords—will go forward as far as possible. The normal trend is toward a clean pupation chamber between two end sheets, one a complete and perfect

cremaster anchorage, the other less complete and more loosely built—a place of exit for the adult moth.

With such adaptability to changed circumstances possible, and such hardiness and manageability, Sylepta would seem to be a good subject for a careful study of the metes and bounds of instinctive behavior. Such not being the aim of this study, let us proceed with this partial life history.

The pupa of Sylepta is about fourteen millimeters long and three millimeters wide at its greatest diameter. It is smoothly rounded on the head end and gradually tapers backward to a very prominent cremaster on the end of the abdomen. The entire surface is reddish brown, and shines like polished mahogany. Several abdominal segments at each end are rigidly sealed, but segments 3, 4 and 5 are freely movable upon each other. The intersegmental membrane between them is always somewhat stretched and always shows as a ring of paler color at each ringed joining. There are no spines or jutting angles on the entire pupa in front of these movable segments, but on them there is a curious development of blunt tubercles at the middorsal line. Two pairs of blunt, heavily chitinized tubercles are rigidly fixed on each segment at the middorsal line with their tips approximated, as shown in Figure 2. In corresponding position on segment 2 there is a pair of minute nipple-shaped tubercles.

The tapered and consolidated rear segments are cross-wrinkled on the ventral side and end in a very prominent cremaster that is armed with eight minute terminal hooks. These hooks are in four pairs, four of them long and four short, set in a single curving row. The two innermost pairs are longer and stronger. Their tips turn ventrally. The two lateral pairs, slenderer but still quite strong, are hooked laterally. The hooks are not barbed, but are smooth and tapering. The outer end of each one is curved like a figure 6, its end forming an almost complete circle.

The living pupa is for a time capable of very extraordinary activity. When disturbed it flings itself wildly about. When at the final molting of the larva, the cremaster is pushed through the loosened skin between the larval drag hooks, its freed eight hooks are worked into the silken end sheet of the leaf roll. They take a deep and permanent hold. I could not detach them. I saw them clearly only after dissolving the silk in KOH solution.

What may be the use of the blunt dorsal knobs on segments 3, 4 and 5 I do not know, but I guess that they may serve to rub off the loosened skin at transformation by pushing and pulling it against the prominent undersurface veins of the Boehmeria leaf. That skin, sloughed off but not further broken, merely crumpled into a little wad, may always be found attached to its hard, empty head capsule, lying close beside the cremaster of the pupa.

As to duration of the pupal stage I give one concrete example. I opened one leaf roll to find in it an inactive larva, white, shortened, thickened, opaque, and obviously ready for pupation. That was on February 21, 1952. I laid the larva carefully back in its unroofed pupation chamber. Next morning (February 22) I found it had pupated overnight. Adding a few fresh leaves to supply moisture to the air in its small glass container I left it undisturbed thereafter. An adult moth emerged on March 3; time, twelve days.

Eggs that may be those of Sylepta I came upon but once during three winter seasons: a little cluster of six, yellow in color and short-columnar in form, octagonal in cross section. They were attached to the under side of a freshly expanded leaf. In hatching, the flattish top of the egg is pushed off, leaving the cup-shaped cell walls clear as cellophane, the eight faces separated by low external ridges.

The new hatched larva is very different in appearance from later instars. It is a stubby little black and yellow caterpillar, with a very big head shaped like a doorknob set on a slender neck-like prothorax. It somewhat resembles the grown larvae of some skipper butterflies (Epargyreus, etc.). Head and prothorax are black, the remainder of the body yellow like the eggs. With the first feeding the body lengthens and becomes green.

I did not succeed in rearing any Sylepta larvae from these eggs. After two of them had hatched and begun feeding, some little yellow Solenopsis ants got into my supposedly tight container and destroyed the lot. But from the many larvae of different sizes that I watched, I conclude that the growth habit of the Sylepta larva is about as follows.

It does not make for itself a leaf roll at first, but feeds more or less openly on the under side of the leaves, skeletonizing them by eating out all the leaf tissues as far as the tougher upper epidermis. Thus clear spots appear in little patches in no fixed arrangement.

Very young larvae are often found feeding inside the leaf rolls of older larvae, often in abandoned rolls, if the tissues are still green. I do not know at what age they begin making leaf rolls. A study instar by instar is still lacking.

So much for the structure and activities of *Sylepta cylindrica* in its immature stages. Now for a brief account of its enemies, both parasites and predators, its competitors and associates during these same developmental stages. I begin with the enemy that I found to be ever-present and very destructive.

Parasites

Bassus texanus

This is a high-stepping Ichneumonid parasite with a wing spread of about 12 mm. It is about half black and half red—head, thorax and wings are wholly black; the abdomen is bright red. The two front legs are black, long hind femora and coxae are red. The female has a slender decurved red ovipositor somewhat longer than the abdomen. Both sexes are conspicuous and diurnally active.

Females may be easily seen at work busily searching the leaf rolls of Boehmeria. They rarely stop on a normally expanded leaf and seemed to avoid the old tattered empty rolls; but they inspected every fresh roll from end to end, with the ever-ready ovipositor unslung and ready to put an egg into any suitable opening.

Noting that they were not much disturbed by my presence, even after a collecting net had been swung to capture one of them, I seated myself on the ground beside a fresh-looking leaf roll that was within reading distance of my spectacles and waited for a female to come along and search it while I looked. One came very soon, and I watched her steadily for at least ten minutes.

First she ran rapidly over the leaf roll from end to end, with her ovipositor unslung, its straight blades and their curved sheath held together at both ends to form a capital D-shaped figure. With the tip of the ovipositor she tried the skeletonized window-like spots from which all the soft tissues of the leaf had been eaten, and found them all closed, the upper epidermis unbroken, and too tough to puncture. Then she trailed the tip of her ovipositor along the sealed outermost layer of the leaf roll back and forth several times full length, prodding

steadily, evidently trying to find a loose place to slip it under the overlap. She could find such openings only at or near the ends of the leafroll. After probing several of these openings she settled down at the end of one, and with her ovipositor deeply inserted in a crevice she prodded steadily for a long time (perhaps five minutes, I was too intent on seeing the act to think of measuring the time); then withdrew her ovipositor and flew away. Perhaps she had laid an egg.

I reared several adult *Bassus texanus* of both sexes. In fact in early January they were becoming more numerous than Syleptas in my rearing jars and for a month thereafter I reared no Syleptas at all. In the little Boehemeria clump that I was watching the parasite had exterminated its host, and also itself, temporarily; but I found a few by searching other clumps elsewhere.

Sylepta makes no cocoon but Bassus makes one: a white oblong-oval capsule, nearly transparent and rounded at the ends. It is attached by irregular tangled threads to the inner walls of the leaf roll. These connecting threads have to be made before the cocoon can be suspended among them, clear of the leaf roll on all sides.

One Bassus emerged as an adult twelve days after it finished spinning its cocoon. As the first visible indication of Bassus infestation, the Sylepta turns whitish, and becomes shorter and thicker. The growth of the parasite becomes very rapid at the last. It consumes completely the flesh of its host, leaving the discarded empty skin squeezed into a little hairy wad that would be hardly recognizable but for the freckled head capsule attached to it. This may always be found outside the Bassus cocoon among its suspensory threads at one end.

Bassus was the only large and overwhelmingly destructive enemy I observed on Sylepta, but associated with it and doing similar damage was a Tachinid fly; three microhymenoptera were sometimes present in small numbers.

The Tachinid fly, *Zenillia boarmiae*, is slightly larger than a housefly and considerably more robust. It is blackish in color and thickly overspread with a whitish powder than forms a complete ring around each compound eye, and on the thorax besprinkles all the broader more convex surfaces except four narrow black lines that run lengthwise on the dorsum. Three broader blackish bands lie crosswise on the abdomen. All its upper surface is beset with conspicuous stiff bristles.

Two adult specimens emerged from Sylepta leaf rolls kept in rearing jars. Two larvae probably of this species were found in other leaf rolls, but both were injured in opening the rolls and neither was reared.

The three microparasites found at different times in my isolated Boehmeria clump were *Tetrastichus modestus* Howard and a new species each of Microgaster and Apanteles. The numerous Tetrastichus specimens all came from three minute, oblong, tight-woven white cocoons found on January 5, 1952. Each cocoon yielded eight adults, all twenty-four of the same sex. Does not this indicate polyembryony, with three successive divisions of the larva that made the embryo into 2, 4 and 8 individuals?

Microgaster n. sp.

This little Braconid parasite was first taken February 11, 1952. It was flying among the lower Boehmeria branches that overhung the water in the ditch, darting in and out and roundabout so irregularly and so swiftly I could hardly say whether I was seeing anything or not; but after many sweeps of a big net I caught one. Once in this bag of the net it surprised me by not trying to fly out; it only climbed up and up. If disturbed it fell back to the bottom of the bag and at once started climbing again. I reached down into the bag with an open cyanide bottle, brought the bottle up from below, and the Microgaster fell into it.

Feeling sure that the little Boehmeria clump was its home, I got a small stiff-rimmed nylon water net that by wig-wagging I could push among the Boehmeria stems and close around their bases. I quickly got a nice series of specimens and sent them to Dr. C. F. W. Muesebeck for the U. S. National Museum collection.

Why so swift and agile a flyer should only crawl for safety was, and continues to be a puzzle to me.

Concerning the new species of Apanteles, I have nothing to add save that some reared adults were determined as such by Dr. Muesebeck.

Other Residents

Leaving parasites aside, there were other residents of my Boehmeria clump in great variety. Of herbivores some were eating leaves, some were sucking sap, a few conspicuous carnivores were ranging through the top, "seeking whom they might devour."

Resident in the Boehmeria tops I found a butterfly larva and a spider.

Vanessa virginiensis, the Painted Lady. On March 14, 1952, in the very top of my most-used clump of Boehmeria I came upon a larva of this world-ranging butterfly. It had done startling damage to several of the crowded plants. There were scattered leaf fragments with much cut-worm-like cross cutting of petioles, and bits of blades were hanging by shreds of their bark. A little spinning of long stay-threads had lifted and fastened together the tips of two large leaves, beneath which canopy the big blackish spine-armed larva rested, or fed betimes under their partial shelter.

After transfer to a moving cage the larva transformed next day, March 15. The pupa, attached by its cremaster to an over-topping leaf, was all pale, but was beginning to show its paired marking of shining gold. Kept for a week under proper conditions, a perfect adult butterfly emerged on March 21. I sent it to Dr. A. B. Klots for determination and for further study of the larvae. Another grown larva of Vanessa was found on April 13th, similarly at work on the top of a robust clump of *Boehmeria cylindrica* some 25 miles north of Lake Placid on Josephine Creek, and this also was reared. Next day two very young larvae were found on my most-used clump by the ditch at Archbold's: black larvae, armed with longitudinal rows of forked spines segmentally arranged, and some of them white-tipped toward the rear. Whole constellations of minute white dots besprinkled the very black skin of the larva. All these larvae were sent to Dr. Klots.

Chiracanthium inclusum. This is a little whitish Clubionid spider which often lives in a top leaf of *Boehmeria cylindrica*. It pulls the outer margins of a leaf downward and fastens them together with white silk. Thus it makes not a roll but a more or less tubular cover for itself open at both ends, the more open end is indrawn, and much more white silk added there. The silk visible at the ends is a ready guide to finding the spider. If the leaf chosen is not fully expanded, its further growth will cause the roll to be high-arched above and wrinkled across the leaf end.

I found a female resting inside a roll with a sphere of eggs beside her almost as big as herself. It is a running spider that as a hunter pursues its prey by night and uses the roll for a daytime resting place. It is common

enough to be of some ecological importance as a nocturnal carnivore.

It is about six millimeters in body length, all white except for its blackish colored face, and tips of all the hairy two-clawed feet.

Cyrtocapsus caligneus Stal. This little aberrant capsid is of the palest possible green color, with very faint brown markings; it lives in the shadowy central part of my Boehmeria clump, among the overshadowed underling shoots. It is wholly invisible among the pale stems. Legs and wing tips are clear as cellophane. There are some faint filmy brownish streaks along the veins of the wings, and black tips on the claws of the tarsi. The dorsum of the thorax is brown. It looks like a detached bit of bark or leaf, camouflage perfect.

I found my first one by accident on February 29, and afterward I swept through the dense center of the clump with a stiff-rimmed net repeatedly and found a few more, among them a nymph, permitting it to be called a resident; dates, March 3 and March 29.

Annotated List of Other Resident Insects

(Excluding thrips, springtails, podurans, mites, and other micros, on which no observations were made.)

Pachybrachius albocinctus (H. B. Barber). A free-ranging carnivore. Family Buprestidae.

Pseudococcus citri (Risso). Family Coccidae. Determined by Harold Morrison. These are little flat scale-like creepers, found on green stems, mainly around the buds; slow moving but not spot-bound; completely covered with white wax in a coat that in delicacy and structural refinement far surpasses the finest work of human hands.

Hyalochoria cavriceps (Reuter). Family Miridae.

Sibovia occatoria (Say); *Deltocephalus sonorus* (Ball); *Haplaxius slossonae* (Ball). Family Cicadellidae. Determined by D. A. Young.

Machlotica n. sp. (Clarke). Family Glyphipterygidae.

I have listed Machlotica last with intent to keep it apart from all the others in accord with its ecological isolation from them all. It lives apart, in the terminal leaf buds only. It has not an enemy in any of them; is not a competitor with any of them. It has neither parasites nor predators so far as I could discover in handling hundreds of living specimens, and rearing many of them. Perhaps it is too small to be of food value to any of them. If edible it might easily be captured for food, when it creeps out from its shelter in the bud, to find a place to pupate.

It will be easily recognizable by the following descriptive notes on the adult and by its developmental stages and their habits.

Machlotica

The larva of this minute bud moth feeds on and inhabits the terminal buds of erect stems and branches of Boehmeria. I did not find it at once when I began collecting leaf rolls, though it was present in greater numbers than they. It kills the bud and stops growth in length of stem. New growth then starts from lateral buds below it, on the green stem. I did not find the egg, but I found holes where larvae had entered and eaten downward.

In terminal buds of Boehmeria each of the paired and opposite leaves has its own pair of stipules between their bases: deciduous stipules that are shed before the leaf becomes fully expanded. At the time the Machlotica larva enters these stipules have about the same size, shape and appearance as the blades of the leaves. The larva enters when leaves and stipules are very closely appressed at the center of the bud. It generally gets inside by eating its way through the middle of a stipule. The outer end of the stipule dies and turns black, but stays in place and is an easy guide mark for finding infested buds. After destroying the growing point of the bud the larva feeds downward as a stem borer, through soft tissues (meristem). Its completed burrow may be an inch or more in depth and is always very irregular in width; for in the bud all is soft undifferentiated plant tissue. Its work in this tissue causes a gall to develop at the end of the stem: a cylindric thickening of the walls. Gall formation stops where wood and bast fiber begin in the walls of the stem and in them the burrowing is confined to the central pith, causing a narrowing of the burrow.

The gall is an oblong swelling that may become three times the diameter of the green stem, but is very inconspicuous, being overtopped by large green leaves. The topmost pair of fully expanded leaves arises low down on the sides of the gall. The cavity of the gall becomes widened and ridged inside by growth of the stem.

The burrow is always irregular, gouged out variously at the sides, not infrequently out to the mark—and when so far out, further growth bursts the wall and the exposed tissues turn black on drying and the larva dies.

The cavity becomes a shelter for little spiders, aleyrodids, springtails, etc. Toward the end of its growth, the larva packs its little pellets of frass down into the unexpanded lower part of its burrow. Still later it carries them out to the surface and builds them into a fragile, black chimney-like structure surrounding its exit hole. Until gall formation the burrow is a rather close-fitting messy tube smeared with a mixture of black frass and liberated plant juices; but the skin of the larva is water-repellent and it comes out clean.

Pupation. The tell-tale blackened scale tip projecting from the center of the fresh green bud makes it easy to discover the infested tips before there is any other sign of infestation. I plucked 100 or more tips at one time for examination. About half of them were empty and abandoned. For the remainder, I clipped off the leaves and exposed the burrow by carefully shaving thin layers off the stem lengthwise. I found living larvae of various sizes in most of them but no pupae in any of them, showing that the larva leaves its burrow for pupation elsewhere. Then I began a search for suitable cover for pupation. I tried soil, sand, sawdust, root tangles, etc., none of which was acceptable, and then to my great surprise, found my first pupae on the under side of a bit of bond paper that lay on top of some fine sawdust. Instead of soft stuff in which to hide and spin a soft cover, it chose a plain, hard surface.

The pupation shelter it made for itself looked more like a miniature woven fish trap of some crude sort than like the usual oblong silken cocoon. Later I found these pupal shelters placed lengthwise on the flat side of the fallen needles of the slash pine, on strips of bark or bits of straws, and sometimes on dried-up bud scales close beside their own emergence holes.

The case is elongate, spindle-shaped, somewhat suggesting a tropical hunter's helmet, drawn out to a point at both ends. Its component silk is not white but khaki colored; not of fine threads, but of irregular cord-like strands. From a central low peak strong irregular ribs radiate down its sides with a very open basket-like meshwork of finer threads between them. Through this network one could see the pupa and the empty skin of the larva lying at one end wadded together and easily recognizable by the empty head capsule attached to it. The

pupa lies loosely on its flat back within this crudely woven shelter. It is colorless and quite inactive.

The duration of the pupal period I determined by isolating larvae found beside exit holes ready for emergence: One caged on March 7th transformed on March 17—period 10 days. One caged on March 8th transformed on March 20—period 12 days.

A few descriptive notes which follow will aid the worker in recognizing the moth and the larva.

The length of the moth to wing tips is three-and-a-half millimeters and the wing expanse almost seven mm. The wings are not spread rooflike when at rest, but are gathered up against the sides of the body, rounding it off above. The head is held low, and the fore wings when at rest are held high for about three-fifths of their length and then abruptly flexed downward so that their tips rest vertically upon a leaf. The flexure causes a crease which covers and hides the long hind femora. No legs show when the moth is at rest.

This is a black insect, patterned with silvery white, increasingly white underneath, with purplish reflections on its back. A blackish band crosses the wings just before their flexure. The back of the thorax is shining black, covered with scales so small and so closely laid that it appears naked. The wings are black, streaked with narrow interrupted lines of silvery white so broken as to suggest the dots and dashes of a telegraphic code. The marginal fringes of the wings have exceedingly long scales, the flexed tips have shorter and stiffer scales.

The tarsi and palpi are black, ringed with white, and the long terminal segment of the labial palps is margined with white. Eyes are white. The under side of the abdomen is silvery white, faintly crosslined with black where the segments join.

The very large hind legs are thin and flat each with two pairs of very long spurs.

The moth can climb readily up the side of a smooth glass cage. When disturbed on the level it first runs on its legs in taking flight.

The grown larva is about five or six millimeters long, grub-like, and patternless; all pale except for its blackish head capsule and prothoracic disc. It is slow-moving and almost hairless. Prolegs under the abdomen and the paired draghooks at its tip are both short and stubby.

Summary

This is an account of the ecological relationship of insects found to be more or less dependent on the common ditchside weed *Boehmeria cylindrica*, with a partial account of the form and activities of the immature stages of two of them: two moths, one a Pyralid, *Sylepta salicalis*, the other a Glyphipterygid, *Machlotica* n. sp.

The Sylepta is a leafroller whose immature stages have not hitherto been made known. It makes several leaf rolls in succession and pupates in the last one used. Parasites and other transiently associated insects are disposed of in an annotated list. Sylepta makes no cocoon, but instead it shuts off a portion of its last roll by two sheets of silk, and between them has a pupation chamber. Two very interesting structural features of the pupa are: (1) paired middorsal, heavily chitinized tubercles on the freely moveable abdominal segments 4, 5, and 6; (2) a strong eight-hooked cremaster at the end of the abdomen, securely attached to one of the end sheets of its pupation chamber. It has a train of parasites, big and little; one of them is *Bassus texanus*, which is discussed in some detail.

The Machlotica is a bud-moth of a genus not heretofore reported from North America. Its larva enters at the center of the unopened bud and eats its way downward into the tissues of the stem, in which it is for a time a gall-maker. It ends its larval life as a stem borer. It leaves the burrow to pupate outside, and makes for itself in some nearby and fully exposed place, a curiously constructed, coarsely woven, straw-colored cocoon which is latticed like a basket of slats or cords. It is depressed in the middle and drawn out at both ends. The pupa lies on its flattened back and is wholly inactive inside the cocoon.

Two moths, living close together on the same plant, could hardly be farther apart in manner of life. Machlotica is among the smallest of Microlepidoptera. I found no enemies, either parasites or predators. Its life in the open for the short period between leaving its burrow and getting under cover of its cocoon would seem to invite predators. Perhaps it is too small to be of consequence to enemies of either sort.

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CHESTNUT REPLACEMENT IN THE SOUTHERN HIGHLANDS

Blight-killed chestnut (*Castanea dentata* (Marsh.) Borkh.) is being gradually replaced in the western North Carolina section of the southern highlands, and a knowledge of the species replacing it is one of the most important problems facing regional ecologists. Permanent cruise lines established in 1934 at the Coweeta Hydrologic Laboratory, in the mountains of western North Carolina, are among the few sets of undisturbed plots in the region that span the period during which chestnut was reduced from a major component of the forest stand to a rarity. Re-cruises in 1941 and 1953 on Watershed No. 41 show that yellow-poplar has been the most important of the replacement species. Ecologic trends here are similar to those on several other analyzed Coweeta watersheds.

Watershed No. 41 was cut between 1918 and 1923, with a lower cutting limit of 15 inches on the stump. It is known that there have been no fires in the area since 1918, and grazing was gradually reduced from that period until 1933, when it was completely stopped.

Watershed No. 41 was typed in 1934 as predominantly oak-chestnut, with areas along the creek channel classified as cove-hardwood. The seventeen $\frac{1}{5}$-acre plots that fall within this watershed form a line transect extending from the bottom of the watershed to the top—3250 to 4250 feet—perpendicular to the general slope and crossing the two main branches of the stream on the watershed.

The most striking change during the 19-year interim is the decrease in stand density in a forest which, because of the heavy cutting between 1918 and 1923, ordinarily should have approached a denser stocking. The principal reason for this occurrence is the gradual reduction of chestnut from approximately 41 per cent of

TABLE I. *Basal area and stems per acre on Watershed 41 in 1934, 1941, and 1953*

(All stems of tree species 0.5" d.b.h. and larger)

Species	Basal area (sq. ft.)			Stems (number)		
	1934	1941	1953	1934	1941	1953
Chestnut (*Castanea dentata* (Marsh.) Borkh.)	53.34	38.48	0.90	464.1	363.2	41.2
Hickory (*Carya* spp.)	18.80	16.11	20.70	138.2	153.8	182.4
Chestnut oak (*Quercus prinus* L.)	10.49	10.14	14.19	75.9	73.8	61.8
Northern red oak (*Quercus rubra* L.)	9.83	9.68	5.18	73.8	62.9	24.7
Black oak (*Quercus velutina* Lam.)	9.57	10.65	17.94	21.2	34.4	71.2
Yellow buckeye (*Aesculus octandra* Marsh.)	4.20	4.37	5.06	8.2	8.5	8.8
White oak (*Quercus alba* L.)	4.19	4.92	2.75	26.5	28.2	33.2
Black locust (*Robinia pseudoacacia* L.)	3.90	3.42	2.06	36.8	48.5	16.5
Yellow-poplar (*Liriodendron tulipifera* L.)	2.94	5.54	12.98	95.3	141.8	152.1
Red maple (*Acer rubrum* L.)	2.00	2.47	3.72	57.0	56.1	56.5
Sweet birch (*Betula lenta* L.)	1.98	2.07	2.96	15.0	15.0	25.3
Scarlet oak (*Quercus coccinea* Muenchh.)	1.50	2.17	6.94	4.7	14.1	10.9
Miscellaneous	6.22	7.30	8.02	135.7	153.5	150.4
Total	128.96	117.32	103.40	1152.4	1153.8	835.0

the basal area in 1934 to less than one per cent in 1953. The release was so gradual that the crowns of the older trees filled out without providing extensive openings in which reproduction could become established.

The cruise data indicate that northern red oak has shown a decrease in both basal area and number of stems per acre during the 19-year period, while black oak has increased more than would be expected. It is difficult to ascertain whether this difference is real or apparent. The change in number of stems per acre was principally in the size classes under 5 inches DBH—size classes in which black oak is difficult to distinguish from red oak. The fact that two of the cruises had only winter characteristics to rely upon, coupled with the known hybridization of these two species in the southern highlands, suggests that a summation of northern red oak and black oak values in Table I is most indicative of the real change in the 19-year period.

Observations indicate that the decrease in black locust was primarily the result of several patches of reproduction being suppressed and later killed by the locust leaf miner.

Most of the species responded favorably to the openings left by chestnut. Yellow-poplar increased from 3 to 13 square feet basal area between 1934 and 1953 and increased in number of stems per acre with many of the yellow-poplars now occupying dominant and subdominant positions in the crown canopy. The oak species in general showed an increase. Although white oak decreased in basal area, the decrease was due to the loss of overmature trees from the stand, and the remaining stems plus reproduction will adequately balance the loss. Hickory species and red maple—to the chagrin of forest managers—also show evidence of replacing chestnut.

The plots were too large to give detailed information on invasion by new species. However, sourwood (*Oxydendrum arboreum* (L.) DC.), cucumber magnolia (*Magnolia acuminata* L.), sweet birch, yellow birch (*Betula alleghaniensis* Britton), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) had invaded areas by 1953 in which they were not present when chestnut was a major component of the stand.

Although it is too early for an equilibrium to be established, the trend to date indicates that chestnut is being replaced primarily by the advancement of species which were codominant with chestnut and secondarily by invasions and the advancement of subordinate species, especially yellow-poplar.

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ECOLOGY OF THE GREAT SALT LAKE DESERT
I. AN ANNUAL CYCLE OF THE DESERT JACKRABBIT[1]

It is well known that the desert jackrabbit, *Lepus californicus deserticola*, shows radical fluctuations in population numbers. In some years they become so numerous that sportsmen have been known to stage great rabbit drives. In other years the population numbers are so low that no such sport is available. The need for a study of trends and causes of such population cycles stimulated the study reported herein. This report is extracted from a background of much field experience not only by the writer but also by 15 to 25 technically trained members of the staff. This background is not treated in this report.

Preliminary investigations leading to this study were made in September, 1952. Four areas were selected for census-taking in western Tooele County, Utah, in the vicinity of a small outlier at the south end of Camel Back Mountain, which we called "Camel Junior." One area was selected on the east side of this outlier and three areas on the west side. These were designed to be censused from time to time to study the trends in the rabbit population. The areas studied were restricted from hunting and grazing and predators were uncontrolled.

This report represents the study of one annual cycle. A theoretical treatment of annual and secular cycles is given by Woodbury (1954: 278, 287). An annual cycle in the case of the desert jackrabbit results from the cyclical periods of reproduction which generally occur in spring and early summer (accumulated data not herein reported). The new generation that appears is then subjected to destructive forces of the environment that drive the numbers downward again. Repeated annual cycles are not exact duplicates of one another. It is hoped that study of future annual cycles will help to delineate secular cycles if they occur. MacLulich (1937) has shown that there are long-time (secular) fluctuations in numbers of the varying hare, *Lepus americanus*.

The study of Green *et al.* (1940) in Minnesota, deal-

[1] This study has been conducted by the personnel of Ecological Research, University of Utah, in its project *Ecology of the Great Salt Lake Desert* and is reported by the Director who appreciates the support given by the staff.

ing with one secular cycle of the snowshoe rabbit is very illuminating. It suggests the ideas that (1) after the numbers of the snowshoe hare population reach a peak and begin to decline, the young that survive are not numerous enough to replace the losses in the adult population, and (2) that when the bottom of the cycle is reached, the young that survive are more than enough to replace the adults that are lost and this trend then leads to another peak.

Methods and Procedures

The first area, "A," 64 acres (25.9 hectares), was laid out on the east side of Camel Junior, as shown on the sketch map, Figure 1, so that a long narrow strip 0.8 mile long and 0.125 mile wide (497 × 77.7 meters) extends from the ledges on the mountain eastward across the flat. The terrain included in the area consists largely of stabilized sand dunes covered with typical sand dune vegetation, mainly four-winged saltbush, *Atriplex canescens,* greasewood, *Sarcobatus vermiculatus,* rabbit brush, *Chrysothamnus,* and others.

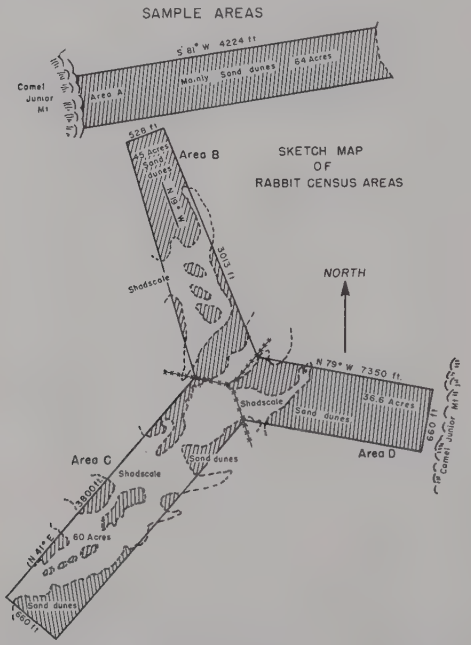

Fig. 1. Sketch map showing rabbit census areas A, B, C, and D. A is east of Camel Junior Mt.: the balance are west.

The three areas on the west side of Camel Junior were so arranged that they converged at fences in the center, as shown on the sketch map. From a central point where a small corral was constructed, three radiating fences were built 120° apart. Three census areas were laid out in radial fashion from the fences as shown. All of the areas were so arranged that each had one end blockaded by the fence so that rabbits would not pass through, or if they did, they could be readily observed.

The north wing, area "B", 45.3 acres (18.3 hectares), contained some sand dunes, roughly about half the area. The balance consisted of flat lands containing shadscale. The southwest wing, area "C," 60 acres (24.3 hectares), included shadscale flats to the extent of about 60% but also contained some irregularly placed sand dunes. The east wing, area "D," 36.6 acres (14.8 hectares), was composed almost entirely of sand dunes covered with the typical sand dune vegetation.

Census Procedures

In attempting to count the rabbits, the drive was made from the open end of the strips toward the barricade at the other end. Men were stationed across the open end of the area with approximately equidistant spaces between them. While the center of the line held still, the men on each side moved forward to make a curved line which approximated a parabola, Figure 2.

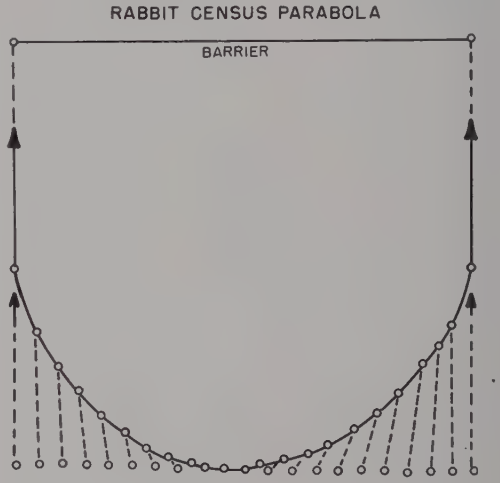

Fig. 2. Sketch showing arrangement of men in parabola to make rabbit census.

Men in this parabola then moved forward toward the other end of the area where the barricade effectively stopped the rabbits.

This arrangement was designed to space the men close enough together so that all of the bushes large enough to hide a rabbit could be scrutinized. The number of men in the line varied from ten to twenty-six at different times in an effort to find the optimum number for best results. In practice, it was found difficult to keep the men equally spaced and in proper curved lines to form the parabola. It required constant attention on the part of the men to do so. Some men naturally walked faster than others and occasionally produced sharp angles in the curve or big gaps between two men.

The man in the center counted the rabbits that passed through the line on each side of him. Those on the left side of the line counted only those that passed on their left. Those on the right side of the line counted only those that passed on their right. Those on the ends counted any rabbits that passed out of the area in front of them. Two men were stationed at the barrier, one on each side, so that the end men of the line moved toward them. They counted any rabbits that moved out of the area, either through the barrier or close to them on the edge of the area.

When drives were first made on the sectors leading

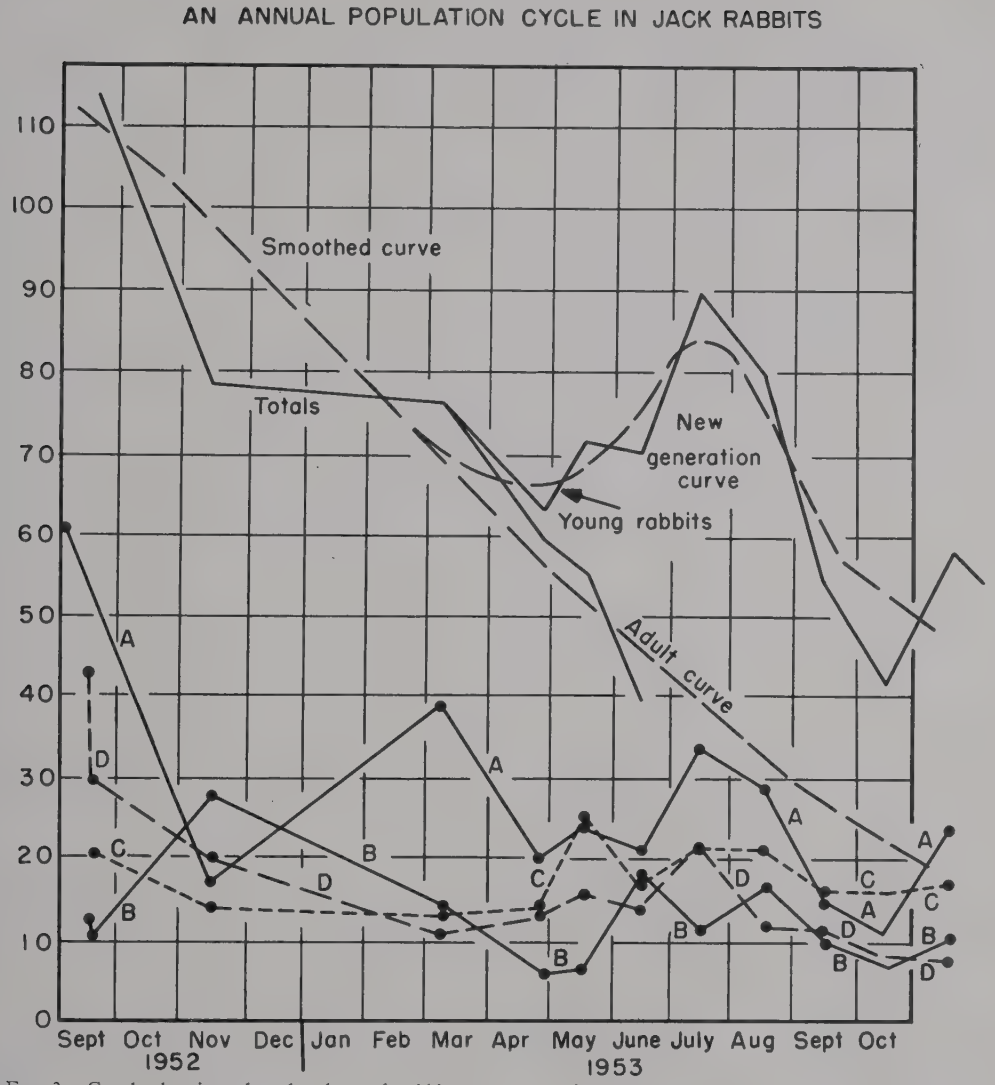

FIG. 3. Graph showing plotted values of rabbit censuses on four sample areas and their totals. The records begin at the time of a rabbit die-off.

to the corral, attempts were made to drive the rabbits ahead of the line and force them into the corral. This proved to be impractical and later was abandoned.

When rabbits were disturbed they usually ran from the line of men toward cover. As the line moved forward and pressed them further, they would usually either run around the end of the line or turn back and break through the line. Most of the rabbits did not take the easy way out around the end, but rather tried to break through, giving the impression that they were well acquainted with their home ranges and would determinedly face the men of the line and try to pass through rather than to leave the known areas of their home ranges.

The first drives were made on several different dates in September 1952. These were followed by drives on 17 November 1952 and 9 March 1953. Thereafter, they were made monthly through November 1953.

RESULTS

The following tabulation shows the numbers of rabbits counted on different dates in the different sectors, together with totals. Young rabbits were segregated during the April, May and June drives, but not at other times. They are not separated in the tabulation but are plotted on the graph.

These figures have been plotted on a graph shown in Figure 3. Each sector is plotted separately to give a curve of its own, and the totals of all are plotted above. This curve of the totals of the four plots is much

Census Tabulation

Areas Acres	A 64	B 45.3	C 60	D 36.6	Total 206
Date 1952					
September 2.....	62	..	..	..	..
September 16.....	..	12	..	43	..
September 18.....	..	11	21	30	..
November 17.....	17	28	14	20	79
1953					
March 9.....	39	14	13	11	77
April 27.....	20	6	14	13	53
May 18.....	24	7	25	16	72
June 15.....	21	18	17	14	70
July 13.....	34	12	22	22	90
August 17.....	29	17	21	12	79
September 14.....	15	10	17	12	54
October 12.....	11	7	16	8	42
November 16.....	24	10	17	8	59

smoother and gives a better indication than the individual plots.

Discussion of Results

Many accumulated observations by several of our staff members (not treated in this paper) indicate that the rabbit population in the general region was at a maximum in 1951 and began to decline in spots in 1952. During the latter summer it had been noted that rabbits were still very numerous in the vicinity of Camel Junior, which was one of the reasons for selection of the areas. By the time the first counts were made it was noted that there were many dead carcasses, especially on Area "A," where the graph shows a rapid decline in numbers between September and November. Field observations indicated that the vacuum left from the die-off had been filled from neighboring areas by March when the numbers had returned to something more nearly normal. Area "B" showed a reverse condition, a heavier concentration in November. Graphs of the four areas suggest that there may be some movement of rabbits from time to time to meet the environmental exigencies. However, experience in the drives leads to the belief that many of the rabbits are sedentary and that they tend to stay localized on their home ranges. Presumably, there must be some environmental disturbance such as overcrowding on the range, shortage of food or the need for shelter to drive them around from place to place.

It was observed in the drives that rabbits were apparently encountered time after time at some spots while no rabbits were encountered at any time in other places. This suggests the idea of preferred localities and supports the idea of home ranges. Apparently the rabbits are solitary, except when mating or when a mother is rearing her young, and they are well distributed singly over the range, apparently in territorial fashion. We have no direct evidence, however, to indicate that a rabbit defends its territory. It may be that they are repugnant to one another, and will not live in close proximity. This might account for the seemingly territorial distribution without assuming that one individual defends its home range against another.

During the April, May and June drives, young rabbits could usually be distinguished from the old ones, but thereafter the distinction was too difficult to be reliable.

On the graph, the smoothed curve of the totals indicates that the adult population of September 1952 gradually declined and would become almost nil at the end of 1953. It is the young, of course, that make the population increase and produce a peak for 1953.

The peak for 1953, however, is much lower than the one for 1952. Theoretically, it should start a decline similar to that of the preceding year and run down to almost nothing at the end of 1954. This suggests the idea that the life span of the rabbit averages between one and two years in length. In this case, there are apparently not enough young rabbits that survived to replace the adults that were lost. If it follows the same pattern as Green's curve in the snowshoe hare, the population number will continue to decline for some additional years.

This decline in population numbers is not necessarily widespread. Die-offs appear to be localized phenomena whose causes are not well understood. Some places have been observed where carcasses are numerous and population numbers low, other places where live rabbits are numerous, and still other places where populations are more normal. It is presumed that heavy populations will tend to overflow into less dense areas but this is a slow process that does not serve to equalize the distribution of rabbits on the range and cannot keep pace with the factors of multiplication and die-offs that provide irregularities in distribution.

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A SHRUB COMMUNITY OF *VIBURNUM LENTAGO*, STABLE FOR TWENTY-FIVE YEARS

Introduction

The purpose of this paper is to describe a small area of a relatively stable type of shrub community, and to relate its practical significance to the maintenance of wildlife cover and of public utility rightofways. The situation and the problem were chosen with considerable care, as representative of a variety of situations involving many regions and many species. It is also representative of certain principles that lie at the root of the rational management of 50 million acres in this country which are being administered by public utility corporations and highway departments, and which could also serve mul-

tiple conservation purposes. Unfortunately, the management of this land has been exploited by chemical manufacturers and spraying contractors, whose practices are not always in harmony with ecological knowledge. The problem is one which not only challenges every student of vegetation in his local region, but puts a professional obligation upon him to apply his knowledge to the public interest.

The area studied is at the Audubon Nature Sanctuary in southwestern Connecticut. It is in the northwestern part of Greenwich Town, Fairfield County, about 6 miles north-northwest of Greenwich village.

The community of *Viburnum lentago* (Nannyberry) occupies an area approximately 15 x 15 meters in a well-drained old pasture which was last grazed about 10 years ago. An area contiguous to the community is moist with seepage in early spring. Today the original pasture is dominated by a dense shrub thicket, with trees varying from 0-100% coverage. Since the abandonment, there has been no apparent disturbance except for a nature trail which bisects the *Viburnum* community.

Geologically, the region lies in the western part of the New England Uplands (Rice and Gregory 1906). It is an area of moderate relief ranging from 300-600 feet in the vicinity of Greenwich. Except for numerous rock outcrops, the bedrock of Berkshire schist is overlaid with ground moraine (Gregory and Robinson 1907, Flint 1929). The region is one of Brown Podzolic soils within a Gloucester-Plymouth area. The soil type at the site of the community is probably a Peru loam (Lunt, Herbert A., ms.). This upland soil type is developed from unstratified glacial till with fair surface drainage and poor underdrainage. It occurs on irregular slopes, and is of wide distribution over the Eastern and Western Highlands.

Vegetationally, this part of Connecticut is commonly referred to as a sprout oak region, which gradually changes to the hemlock-white pine-northern hardwoods of central and northern New England. At the Audubon Sanctuary, sprout hardwoods, chiefly oaks, (*Quercus rubra, Q. alba, Q. velutina*) characterize the uplands. Transitional and northern hardwoods favor the ravines and lower slopes, although both beech (*Fagus grandifolia*) and hemlock *Tsuga canadensis*) can grow on drier sites. As the old fields are abandoned in this section, they usually return to a forest quite rapidly. After a typical herbaceous stage of annuals and perennials, shrubs such as sumac (*Rhus glabra, R. copallina, R. typhina*), bay berry (*Myrica pensylvanica*), and shrubby dogwoods and viburnums (*Cornus* and *Viburnum* spp.) gain dominance. Where present, dominance is later taken over by trees such as gray birch (*Betula populifolia*), red cedar (*Juniperus virginiana*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). However, in some instances various oaks and hickories are also present and will probably survive the shorter-lived trees. In this study, an old-field phase, coincidentally composed of pure *Viburnum,* is proving itself essentially stable.

The authors wish to thank Mr. Charles Mohr, Director of the Audubon Nature Center for his interest in the project and his cooperation during the investigation.

Methods

The senior author was resident at the Audubon Center during the summer of 1952, and the site is well-known to both authors. Data were obtained by the senior author during three man-days in 1952, and are those primarily reported upon here. In 1953, the authors spent two man-days in establishing, mapping, and photographing two 3 x 3 meter permanent quadrats.

In 1952, approximately one-third of the stand was included within three temporary 5 x 5 meter quadrats. Diameters of transgressives and taller shrubs (*Viburnum lentago* and *Rhus typhina*) were measured at 4.5′ (DBH) unless branches diverged from the main axis below this height, in which case diameters were taken just below the point of divergence. The cover transect method (Bauer 1943) was also used to record transgressive and taller shrub cover along a base line through the stand and extending into the surrounding thicket. Within the 5 x 5 meter quadrats twenty ½ x 2 meter quadrats were laid out and percentage cover of lower shrubs, herbs, and mosses recorded. Sprout, sapling (over 1′ high and less than 1′ DBH) and "seedling" (shoots 1′ or less in height, regardless of age of root system) counts were also made in these smaller quadrats.

Comparative light and temperature data were taken in the *Viburnum* thicket, a surrounding sumac thicket, and the upland hardwood forest. Soil samples were collected and pH recorded by the Beckman pH meter.

The nomenclature used for vascular plants is according to Fernald 1950.

Structure of the Community

The shrub, *Viburnum lentago,* is dominant forming a continuous closed shrub canopy 15-18′ in height (Fig. 1, 2; Table I). In 75 sq. meters, a total of 108 stems had an average DBH of 1.7″. The largest specimen, 2.7″ was approximately 26 years of age. Many of the stems occur in clumps; others are closely spaced and originate from a common root system. The stems usually branch 4-5′ above the ground and many of these lateral branches as well as root suckers die back and eventually accumulate on the ground (Fig. 1). Other species found in this stratum included four stems of staghorn sumac (*Rhus typhina*) 3-3.5″ and one each of three transgressives, an American elm (*Ulmus americana*) 1.6″, a white ash 4.6″, and a black cherry approximately 4″. However, the two latter species occurred in the peripheral region of the stand. A grapevine (*Vitis* sp.), although not recorded in the quadrat data, occupied several square feet of cover in the *Viburnum* canopy.

In regard to reproduction, *Viburnum* was most important. It reproduces primarily by root suckers; a total of 237 were counted in 20 sq. meters. Tree seedlings and saplings were rare; only 7 seedlings and 4 saplings of white ash were recorded. The former were very small and of low vitality. No other tree reproduction was found.

The lower shrub layer (12″ high or less) is almost nonexistent, with shrubs covering only 6 per cent of the total area. Of the four species present, poison ivy (*Rhus radicans*) is most important, occupying 4 per cent of the area and occurring in over 50 per cent of the quadrats. Other scattered shrubs of minor importance include Virginia creeper (*Parthenocissus quinquefolia*); oriental bittersweet (*Celastrus orbiculatus*); and Japanese barberry (*Berberis thunbergii*). A total of 94 per cent of the area is unoccupied by lower shrubs.

Herbs are practically absent except for occasional specimens of jack-in-the-pulpit (*Arisaema* sp.); sedge (*Carex* sp.) and Canada mayflower (*Maianthemum canadense*). In this layer, 99 per cent of the soil is unoccupied by herbaceous cover.

In the moss layer, 97 per cent of the area is unoccupied. Scattered mosses and liverworts occupy 3 per cent of the exposed soil.

FIG. 1. *Viburnum lentago* shrub community. Note closely spaced stems frequently originating from a common root system. Branches and small twigs litter the ground. Note paucity of leaves and duff. Clip board with paper for scale. Photograph taken August, 1952.

TABLE I. *Density and percentage of total basal area of shrubs and transgressives based on three 5 x 5 meter quadrats.* Prunus serotina *(x) represented by a single specimen on periphery of stand*

	Density	% Basal area
Shrubs		
Viburnum lentago	108	84
Rhus typhina	4	10
Transgressives		
Fraxinus americana	1	5.
Ulmus americana	1	0.6
Prunus serotina	x	—

Under the entire stand, the exposed moist soil was practically devoid of leaf litter, although branches and smaller twigs of the *Viburnum* had accumulated. On the exposed soil surface, earthworm castings were very abundant. Within the top 6" the soil acidity was pH 5.3 and 5.4 in the *Viburnum* thicket and surrounding sumac respectively. Light readings in the thicket were comparable with those of the upland forest, while in adjacent sumac there was 18 times more light penetrating the canopy. Temperatures within the 1 meter level of the *Viburnum* stand were usually 2-3° F. cooler than in the surrounding sumac. Temperatures in the upland forest and *Viburnum* stand were comparable.

Surrounding the *Viburnum* thicket on the south and east, sumac 18-20' in height and oriental bittersweet form a dense thicket (Fig. 2). In the openings, goldenrods (*Solidago* spp.); poison ivy, and Japanese honeysuckle (*Lonicera japonica*) form a continuous ground cover. To the north and west, larger trees of white ash, American elm, and red maple (*Acer rubrum*) are most conspicuous (Fig. 2). Shrubs frequently found include winterberry (*Ilex verticillata*); grape vines, spice bush (*Lindera benzoin*) and poison ivy. Sensitive fern (*Onoclea sensibilis*) is the characteristic herb.

ORIGIN OF THE COMMUNITY

On the basis of the quadrat data, and from general inspection of the commuinty itself and the surrounding vegetation, it would appear that the *Viburnum* was started as one or several seedlings not less than 2 or 3 decades ago, and possibly very much longer. The age of the root systems is not known, and they may have survived many farming operations. It is unlikely that any trees have been co-dominant with the shrubs during the life of the present crop of above-ground shoots, for if so they by now should have overtopped the *Viburnum*. Other trees which did not at once attain co-dominance may have permanently lost their initial opportunity, and may now be persisting only as short-lived shoots.

Judging from the distribution of other shrubs in the local region, it is difficult to assume that other species were not originally present with the *Viburnum*. At this time, however, there is no evidence of any such shrubby associate except *Rhus typhina*. The shade, density, height and other characteristics of this stand, as compared to those of other shrub species, make it probable that they gradually lost out in competition through the years. The present status of *Rhus* is indicative. Several of the large overtopping stems were broken off by storms between the summer of 1952 and 1953. Resulting etiolated root-suckers have been kept nipped off by rabbits; similarly arising root suckers were observed in other parts of the community; there is no indication that *Rhus typhina* can regain its former dominance.

There is no evidence other than that this community arose through the fortuitous distribution of one or several *Viburnum* propagules at some time in the distant past, and by the gradual elimination of other woody plants that may have been in competition with it.

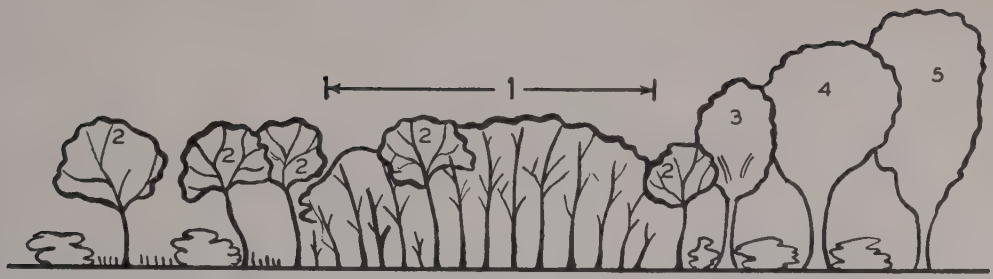

FIG. 2. Diagrammatic representation of the *Viburnum* thicket at Greenwich in relation to surrounding vegetation. Area shown between arrows represents *Viburnum* area. The numbers correspond to the following species: (1) *Viburnum lentago;* (2) *Rhus typhina;* (3) *Ulmus americana;* (4) *Fraxinus americana;* (5) *Acer rubrum.*

FUTURE OF THE COMMUNITY

The *Viburnum* thicket has apparently been in existence for a quarter of a century as a self-perpetuating shrub type. Some of the tallest, oldest *Viburnum* stems are dead or dying, and will be replaced by younger stems, with no change in the over-all height or appearance of the community. One- or two-year-old shoots of *Viburnum, Rhus,* and possibly other woody plants, are being kept nipped to the ground by rabbits; and rabbit-pressure is undoubtedly a critical factor in the openness of the lower strata.

The significance of the two transgressives on the periphery of the stand and the several white ash sprout-seedlings, should be interpreted with caution in view of the very small area studied. The transgressives, barring accidents, would presumably grow to maturity and change at least a portion of the area into forest. On the other hand, the presence of seedlings of one species in a community of another species is never an assurance that even a certain percentage of those seedlings will mature. It seems reasonably certain, however, that the *Viburnum* thicket is not "permanent," and that eventually, in 30, 60 or 90 years, an occasional tree will break through and convert the area to forest. On the other hand, the number of such maturing trees of the past 25 years has been so small that economic control of them, as by artificial means, would appear to be an extremely low-cost procedure requiring attention only at intervals much greater than a decade.

WILDLIFE VALUES

Viburnum lentago, and the other viburnums as well, have usefulness throughout the eastern United States and on the Pacific coast as food and cover for various forms of wildlife, especially for the eastern ruffed grouse. (Martin, *et al.* 1951.) The highly ornamental flowers appear at various seasons, and fruit ripens in late summer and fall, often advantageously hanging through the winter months. The needless destruction of this shrub, as from the sides of rightofways, is obviously an action that should be opposed by those interested in wildlife populations. Furthermore, the botanical stability of this type, as opposed to the quick tree reinvasion of bare areas, leads to cost-maintenance factors that even further point out the irrationality of the unnecessary destruction of this species on land where it can be tolerated.

RIGHTOFWAY VALUES

The American Museum System of Rightofway Vegetation Management, in commercial operation since 1950, is predicated on the botanical fact that in forest regions different non-forest vegetation types become invaded by specific kinds of trees at different rates. The System (Egler 1949, 1954a, 1954b; Pound and Egler 1953) aims to develop that type of vegetaiton within the physical needs of the rightofway which is: of lowest cost, for the most years, with the highest conservation values. In most instances, it has been found that shrub-dominated vegetation tends to resist invasion by tree seedlings, whereas upland eastern grasslands are relatively open to invasion by pines, ashes, maples, elms, birches and tulip poplar. It has been found that the majority of woody plants of the so-called later "stages" of old-field "succession" have not been currently invading. To the contrary, it appears that they had invaded at the same time as or previous to the earliest stages. For these reasons there is little concern at this time for the reinvasion of such woody species.

The physical needs of the rightofways are indicated in Figure 3. In the central portion, low shrubs such as huckleberries and blueberries can be tolerated, which will not interfere with repair and maintenance of the line. Preferably a grassy foot trail should also be present. Concern for the sides, on the other hand, is mainly for trees which may grow into or fall into the wires, or which may be in the way of the wires when they sag or swing. In addition, the utility companies prefer to leave demarcated the full width of the rightofway, which makes undesirable the presence of potentially tall trees on the sides. On these sides, tall shrubs may be tolerated. Permissible vegetation on a rightofway is thus seen to be a maximum concentration of edge effects and border phenomena from the standpoint of wildlife cover, at the same time that it is a combination of the more stable non-forest types and thus cheapest to maintain through the years.

The role of *Viburnum lentago* is now apparent. Since its average height is 10-15 feet, it is ideally suited for the sides of rightofways, where its high wildlife and ornamental values improve public relations, and where its stability (resistance to forest invasion) results in a maintenance cost in this instance of $0.00 for 25 years. The unnecessary removal of shrubs such as these, which is now in progress over thousands of acres along our public utilities rightofways, is botanically and financially unsound, since the shrubs will take over the major job of future maintenance if given the opportunity.

SUMMARY

1. A pure stand, about 15 x 15 meters in size, of *Viburnum lentago,* was considered to have arisen fortuitous-

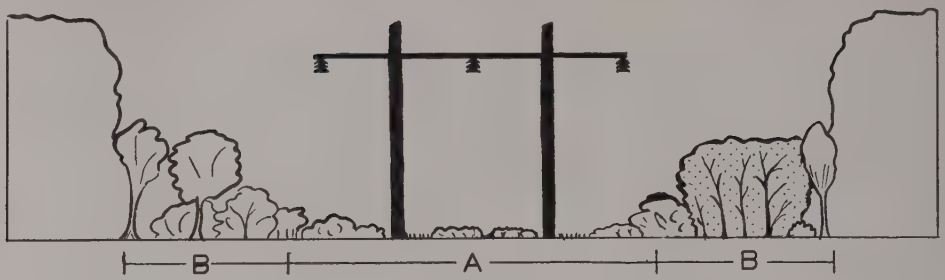

FIG. 3. Diagrammatic cross-section of right-of-way showing low shrubs and scattered grasses under the wires (A) with larger shrubs and low understory trees from the outer wires to the adjacent forest (B). A feasible location for *Viburnum lentago* (stippled) is shown at the right in Zone B.

ly at least 25 years ago, with other shrubs, if present, dying out in competition.

2. As based on quadrat studies, the stand is essentially one-layered, and relatively pure. Small shrubs, herbs, mosses, and seedlings are unimportant.

3. There are few and uncertain evidences of an invading tree stage, and the community appears relatively stable and self-perpetuating.

4. The species has high wildlife values, and physically is suited for the sides of the rightofways of utility corporations, where its preservation, if it already occurs, will improve future low-cost maintenance, public relations, and conservation values.

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MEASUREMENTS OF PLANKTON FEEDERS IN RELATION TO GROSS PRODUCTION[1]

These notes summarize exploratory efforts seeking plankton feeders that might, through their growth rates, serve as indicators of phytoplankton abundance. Growth observations were made on the barnacle, *Balanus improvisus*, the oyster, *Crassostrea virginica*, and the sea squirt, *Styela plicata*, at three stations along the axis of Alligator Harbor. One station was near the mouth; one about 1½ miles up the harbor; and one was near the upper end of this estuary, being an additional 1½ miles farther along.

Alligator Harbor is a shallow basin with depths rarely exceeding eight feet. The tributary flow into this estuary is small whereas there is considerable ebb and flow of Gulf waters through the wide mouth. With these conditions there is practically no vertical stratification and horizontal gradients in salinity and temperature are relatively minor. There is, however, a greater circulation and water exchange near the mouth than toward the head and generally a lower concentration of phytoplankton toward the mouth than toward the head waters. Thus the following contrasts are outstanding:

Station near harbor mouth: greatest circulation, least phytoplankton
Station near mid-harbor: intermediate in both respects
Station near head of harbor: least circulation, most phytoplankton.

Data supporting the above generalizations are presented in Table I and Figure 1, the latter giving chlorophyll measurements as an index of phytoplankton abundance. The detailed composition of the phytoplankton populations at these stations is little known; however, some information is available from studies reported elsewhere

[1] Contribution No. 26 of the Oceanographic Institute of Florida State University.

TABLE I. *Surface salinity, ‰, surface temperature, °C., and Secchi disc depths, meters, near the mouth, at mid-Harbor and near the head of Alligator Harbor covering the dates involved for these observations. Number of readings given in ( ) when entry is an average of more than one.*

Date (1953)	Sal.	Near mouth Temp.	S.D.	Sal.	Mid-Harbor Temp.	S.D.	Sal.	Near head Temp.	S.D.
February 7	....	....	...	....	....	...	30.7	16.5	...
February 14	31.4(3)	15.4(3)	...	31.1(3)	15.5(3)	...	31.1(3)	15.2(3)	...
February 27	28.9(3)	17.4(3)	...	29.7(3)	17.0(3)	...	30.0(3)	17.7(3)	...
March 8	30.1(3)	18.9(3)	...	30.5(3)	18.9(3)	...	30.0(3)	19.3(3)	...
May 21	24.2	26.9	2.3	26.8	28.4	1.4	29.7	28.1	0.8
May 25	26.7	29.4	2.3	27.6	29.9	1.5	27.8	30.4	0.8
May 29	30.7	27.9	0.9	31.6	27.7	0.9	29.3	27.9	0.6
July 5	30.4	30.8	0.9	30.6	30.5	0.6	30.3	30.7	0.5
July 14	32.1	28.7	2.0	31.3	28.1	1.1	30.0	27.9	0.5
July 21	29.4	30.9	...	29.7	30.7	...	32.1	30.4	...
July 27	31.5	29.9	1.7	31.7	29.9	0.9	31.3	27.9	0.6
August 3	32.1	31.1/	...	31.8	31.9	...	31.0	31.7	...

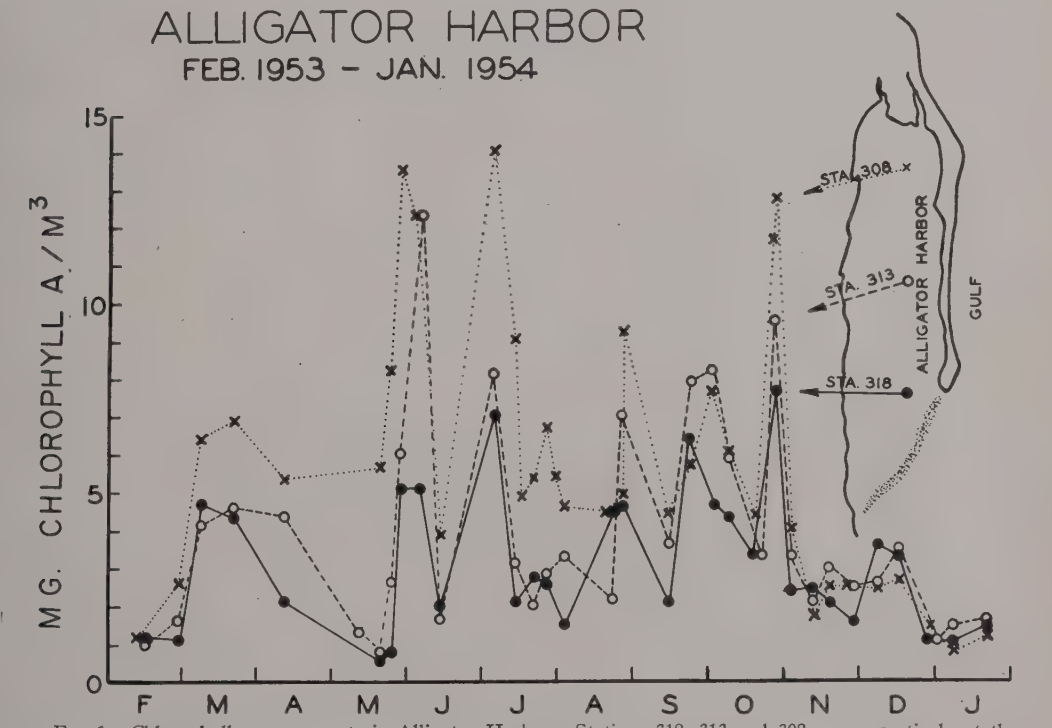

FIG. 1. Chlorophyll measurements in Alligator Harbor. Stations 318, 313 and 308 are respectively at the mouth, at mid-Harbor and near the head of the Harbor and are the same stations used for growth data and for the hydrographic observations of Table I.

(Marshall, in press). The following comments on the phytoplankton in Alligator Harbor are offered as pertinent to this discussion:

The majority are nannoplankton diatoms, many being naviculoids. They are unattached types associated with the bottom; however, through mixing they are constantly changing back and forth from a benthic to a planktonic state.

Judging from the shallower waters toward the head of the harbor and the higher turbidities there, it appears that the mixing which brings such benthic forms into the plankton is greatest toward the head and least near the mouth. Associated with this mixing and turbidity is an abundance of plankton fragments and organic detritus.

In spite of their lesser numbers, species of *Rhizosolenia* and various other large marine phytoplankters are frequently present in sufficient mass to form an important component of the total plankton.

Though it is improbable that the populations are homo-

TABLE II. *Growth of* Balanus improvisus *at three stations in Alligator Harbor, 1953.* Orifice "area"* of largest specimens in sq. mm.

	Feb. 7				Feb. 14			Feb. 27			March 8		
	Mean	N.	s		Mean	N.	s	Mean	N.	s	Mean	N.	s
Sizes from	0.3	20	±.05	Harbor mouth....	1.0	20	±0.20	5.6	20	±1.07	8.6	20	±1.12
3 slides at	0.3	20	±.05	Mid-Harbor.....	1.0	20	±0.14	5.1	20	±0.70	10.4	20	±1.88
beginning	0.3	20	±.03	Upper Harbor.....	0.9	20	±0.10	4.7	20	±0.74	11.5	20	±2.06

	May 21				May 25			May 29		
	Mean	N.	s		Mean	N.	s	Mean	N.	s
Sizes from	0.3	20	±0.10	Harbor mouth....	2.1	7	±.30	Lost	..	.....
3 slides at	0.2	20	±0.10	Mid-Harbor.....	2.4	20	±.83	5.5	16	±1.22
beginning	0.2	20	±.03	Upper Harbor.....	3.0	9	±.66	11.5	11	±2.44

*"Area" is used here to denote the length X width of the orifice.

geneous and uniform, studies to date have not revealed major qualitative differences in plankton at the three stations used for these growth comparisons.

Most of the growth observations involved the barnacle. To collect sets for this work slides of tempered masonite (with both surfaces smooth) were suspended vertically in floating racks near the marine laboratory pier. Once a set of young barnacles had established itself a few slides were preserved immediately and the rest distributed at the three stations, being held vertically in wooden racks suspended about one foot below the surface. On subsequent visits to the stations, slides of these barnacles were removed and preserved, thus providing specimens indicative of the growth attained since being placed on station. To avoid confusion from rapidly growing barnacles of later secondary sets, only the largest barnacles on each slide were measured. Usually it was easy to find twenty such large barnacles for these measurements but occasionally fewer were available. The length and the width of the orifice were taken and the product, referred to as "orifice area," was used as a measure of size. Basal measurements were not used since these are so obviously altered by crowding.

The measurements obtained in this manner are given in Table II. For both sets that were followed, contrasts became increasingly apparent with time, showing the greatest growth toward the upper end of the Harbor. Subjecting the more contrasting measurements to the *t*-test leads to the following conclusions. There is better than a 99% probability that the measurements recorded for the harbor mouth and mid-harbor stations on March 8 represent a true population difference but the probability of a true difference between mid-harbor and the upper station as of that date is not much better than 90%. Also, there is a better than 99% probability that the measurements for the mid-harbor and the upper harbor stations on May 29 represent a true population difference whereas the seemingly great contrasts on May 25 give low *t* values because of the limited numbers.

Thus the data, though limited, tend to indicate more rapid growth at the stations where the higher chlorophyll measurements indicate a richer phytoplankton population. If circulation rates, within the limits common at these stations, affect growth rates, this influence tends to be obscured by the contrasting effects of the different phytoplankton levels.

The oysters studied were placed in floating cages about one foot below the surface at the three Harbor stations. The data obtained are given in Table III. Though they suggest greater growth toward the headwaters, the growth differences observed are judged to be within the range of error inherent in the procedure.

TABLE III. *Growth of* Crassostrea virginica *in cages at three stations in Alligator Harbor.*

	Mean displacement volume/oyster*		
	July 5 1953	Aug. 3 1953	Increase
Harbor mouth....	12.2 ml (50)	16.9 ml (47)	39%
Mid-Harbor.....	12.2 ml (50)	17.6 ml (46)	44%
Upper Harbor....	11.6 ml (50)	16.8 ml (44)	45%

*Measured displacement of entire lot and divided by no. of individuals involved as given in ( ).

The attempt to procure growth data on sea squirts failed because, with budding and the anatomically interconnected clusters that form, the history of individuals could not be followed.

Costlow and Bookout (1953) reared *Balanus improvisus* on pure cultures of *Nitzchia closterium* and of *Chlamydomonas* sp., also on mixtures of the two, and found the uni-algal cultures of *Chlamydomonas* to be the most favorable. Such food preferences do not nullify, however, the possibility of observing gross production relationships between mixed plankton associations and the growth of sessile plankton feeders, using the latter as a tool to judge the magnitude of the former. Certainly the barnacle looks promising in this respect; however, excessive technical difficulties, such as led to the discontinuation of the observations reported here, are discouraging from the practical standpoint. I lost much time being unable to get good sets to work with, and once sets were obtained and placed on station, the work was often negated by predation, other mortalities, storm losses and perhaps thefts of the mooring rigs.

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MICROCLIMATOLOGICAL FEATURES OF AN OLD FIELD AND AN OAK-HICKORY FOREST IN NEW JERSEY

On the Piedmont of New Jersey, there are many fields which are no longer cultivated and are in some stage of secondary succession. Bard (1952) has described various ones in this area which ranged from 1 to 60 years of abandonment. After 40 years of abandonment, the field can be described as a mosaic of scattered islands of herbs in a matrix of encroaching clumps of trees and shrubs. It is a mosaic of habitat extremes.

The mature forest in this vicinity is an oak-hickory community, one stand of which, Mettler's Woods, although at one time subject to fire, has remained as forest since Indian days (Buell, Buell, and Small 1954). Where its canopy is continuous, habitat extremes are at a minimum.

The objective of the present study was to measure temperature at several levels in what are apparently the most extreme habitats in a field 40 years after abandonment and to compare these temperature measurements with similar records from Mettler's Woods. Although it was obvious that there are large differences, the question to be answered was how large and what differences at various levels above the ground in relation to local vegetation structure.

The study area was located approximately one mile east of East Millstone, New Jersey (40°30'N, 74°34'W). The terrain here is gently rolling and the soil is quite uniform so that the sites were comparable as to both exposure and soil. Observations were made from August, 1951, through August, 1952.

One location in Mettler's Woods was selected. Data are also presented for two contrasting locations in a 40-year field, one under a small red maple tree in a thicket and the other in the center of a grassy opening surrounded by thickets of shrubs and young trees.

Air temperatures were measured at 2 m., 20 cm. and 5 cm. heights above the ground using standard maximum and minimum thermometers placed in double aluminum shields, the same equipment as described by Cantlon (1953). Soil temperatures were measured at a depth of 4 cm. below the surface by placing standard maximum and minimum thermometers in horizontal chambers supported by metal shields on top and sides. Temperatures were read weekly. All temperatures are given in degrees Fahrenheit.

The vegetation immediately surrounding the station in Mettler's Woods was relatively uniform. The oak canopy (consisting of *Quercus alba*[1] and *Q. rubra*) was about 60 per cent complete in all directions. The flowering dogwood (*Cornus florida*) was almost continuous, with 99 per cent measured cover. The shrub layer of maple-leaved viburnum (*Viburnum acerifolium*) afforded no cover over the instruments but did form a shield from wind movements. In the herb layer, the may-apple (*Podophyllum peltatum*) covered from 20 per cent to 30 per cent of the ground on the south and northwest of the instruments in spring, but during June the plant rapidly deteriorates so that by July it had lost its importance as a ground cover.

The field station in the grassy opening was located where the trees and larger shrubs were absent for a radius of about 6 m. The opening was surrounded by trees of red maple (*Acer rubrum*), eastern red cedar (*Juniperus virginiana*) and black cherry (*Prunus serotina*) of various sizes up to 15 to 30 feet high. Clumps of bayberry (*Myrica pensylvanica*) were dispersed on the periphery, and tufts of little bluestem (*Andropogon scoparius*) occurred throughout the center.

The station under the maple was located just outside the southwestern boundary of the opening and about 20 m. from the location of the thermometers in the opening. The maple was about 3 inches DBH and about 15 feet high. It was in a group with other trees, red cedars and flowering dogwoods, as well as large shrubs of bayberry. The ground was covered with a thin leaf litter. Scattered shoots of poison ivy (*Rhus radicans*) dominated the lowest layer.

Air temperature extremes during the course of the year's study decreased in intensity from the grassy opening (—8° to 112° F.) to the thicket (— 8° to 100° F.) to Mettler's Woods (—3° to 96° F.). As with the annual extremes, the weekly extremes were in general in the same order of difference for the three stations. However, at the various levels above ground, conspicuous differences appeared. At the field station in the grassy opening, the greatest variation in maximum temperature was noted in the spring, summer and fall. During this period when the sun was rising to, and falling from its zenith (73°), the warmest temperatures were found at the 5 cm. and 20 cm. levels. When the angle of inclination of the sun was lowest (26°) in winter, the variations in maximum temperatures at the 5 cm. and 20 cm. levels were least. The lowest minimum temperatures were found at the 20 cm. level throughout the year. During the spring, the highest minimum temperatures occurred at the 2 m. level. On several occasions during the winter, marked differences in minimum temperatures between the 20 cm. and the 5 cm. levels corresponded to periods of snow cover, the higher level having lower minimum temperatures at these times.

At the field station under the maple, the seasonal variation in maximum temperatures followed, in general, those conditions found in the grassy opening but the extremes were not so great. A striking departure from the temperature pattern found in the grassy opening could be observed in mid-May at the maple station. At this time, when the canopy closed, a reverse of the maximum temperature gradient of the opening was established. Instead of an increase in temperature toward the ground, the highest readings were observed at 2 m. and the lowest maximum temperatures were found at 5 cm. The differences of minimum temperature within the sampling levels were less pronounced under the maple during periods of snow cover than those found in the opening. Although the lowest minimum temperatures were generally found at 20 cm., as in the open, this occurrence was less consistent under the maple.

Soil temperatures at 4 cm. depth showed slightly greater annual variation at the stations in the field (30° to 90° F. in the opening and 28° to 79° F. in the maple thicket) than in Mettler's Woods (29° to 73° F.). Conspicuous seasonal differences also occurred. In the opening, the greatest variation between maximum and minimum extremes occurred during the spring, summer and fall, paralleling the pattern of air temperatures. In Mettler's Woods the difference between them was uniformly less and was least in the late spring and summer when the forest canopy was closed. The thermal extremes were also less under the maple in the thicket than in the opening.

[1] Nomenclature for all plants follows Fernald (1950).

The nearest Weather Bureau station is located 8 miles east, on the agricultural campus of Rutgers University in New Brunswick. The records for the period corresponding with this study show the extremes during the year's period to be 3° F. minimum and 99° maximum. Compared with the grassy opening (—8° F. to 112° F.) the differences are large. Wolfe, *et al.* (1950) found similar pronounced differences between records which they took in the vegetation and those recorded at the nearest weather bureau station.

When the snow cover was deep enough to cover the lowest set of air thermometers at 5 cm., the insulating effect of snow cover was recorded. Relatively higher temperatures were maintained at this level ranging from 5° F. to 15° F. warmer. The refrigerated air passing over the snow, however, caused the 20 cm. level temperatures to drop to their lowest readings, the minimum reached at this time being —8° F.

The effect of the canopy on air temperatures could be observed in several respects. In Mettler's Woods and under the maple, the increase in temperature with height above the ground during summer and the decrease with height during the winter, appeared to be related to the presence or absence of canopy interference.

In the immediate vicinity of the instruments at the station in the opening, the dominant ground cover was little bluestem. This one-meter-high grass grows in bunches, and the dense fibrous roots eliminate all but the low-growing plants and lichens between the clumps. The woody vegetation surrounding the grassy opening allowed a maximum amount of insulation at and near the ground and an accompanying minimum of air movement. This would seem to account for the higher maximum observed at the 5 cm. and the 20 cm. levels during the spring, summer and fall. Lower winter differences in maximum temperatures were probably caused by the interception of the low winter sun by stems of surrounding trees and shrubs. Both the minimum temperatures found consistently at the 20 cm., and the maximum temperatures found at the lowest levels are in agreement with Geiger's (1950) summary of incoming and outgoing radiation in vertical and horizontal types of plant cover.

Summary

1. Weekly readings of maximum and minimum thermometers taken in a mature oak-hickory woods and in two habitats in an old field abandoned for 40 years, a grassy opening and a small thicket of young trees and large shrubs, show pronounced annual and seasonal temperature differences between themselves and between them and the local Weather Bureau station.

2. Records taken at 5 cm., 20 cm. and 2 m. levels as well as 4 cm. below ground show also that within these habitats, microclimatic structure from season to season is very different from one to another.

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NOTES ON THE FOOD OF *CRASPEDACUSTA SOWERBII* IN CRYSTAL LAKE, RAVENNA, OHIO

Medusae of the fresh-water jellyfish, *Craspedacusta sowerbii* Lankester have been recorded from many localities in Europe, Asia, Australia, North America, Central America and South America. Perhaps they are cosmopolitan in temperate and tropical regions. Usually they occur in artificial or natural ponds, sometimes in rivers, and occasionally in lakes as large as Pymatuning Reservoir (Jackson 1953).

Ordinarily the medusae occur sporadically in small numbers only, but sometimes they swarm by the thousands. In spite of their occasional availability, there have been few published reports on their food, and apparently no published quantitative studies. The earliest qualitative report of the food of this interesting animal was given by Lankester (1880a, 1880b, 1880c), who stated that both he and Mr. Sowerby had observed them feeding upon *Daphnia*. The same author (1881) described intracellular digestion, and mentioned the presence of algae in the endodermal cells.

Subsequently, qualitative descriptions of the food were given by Boecker (1905), who observed Infusoria, filamentous algae, *Amoeba*, etc. in the stomach; by Boulenger and Flower (1928), who said that young medusae fed upon plankton organisms; by Dejdar (1934), who found *Bosmina* and *Keratella* (= *Anuraea*) *cochlearis* in those rare cases where he encountered anything in the stomach of his specimens; by D. W. Dunham (in an unpublished Ph.D. dissertation at Ohio State University, 1941), who found that young medusae fed upon rotifers, and that adults consumed *Daphnia, Bosmina, Cyclops* and *Diaptomus;* by Dexter *et al.* (1949), who reported that "cladocerans and copepods were found entangled in the tentacles"; by Thomas (1950), who reported that his Australian specimens fed in the laboratory upon daphnids, cyprids and small mosquito larvae; and by Symoens (1953), who stated that the nourishment consists chiefly of rotifers and larval copepods.

In addition to published studies, M. K. Linscheid (in an unpublished M.S. thesis at Western Reserve Univer-

sity, 1935) gave detailed quantitative estimates of the stomach contents of a number of medusae. With the exception of one specimen which contained a single midge pupa, she found only *Bosmina* in the stomachs of her specimens, varying in number from two to 48 per individual (her average was 14.6 *Bosmina* per individual). The value of her estimates, however, was reduced by the fact that observations were made only "an hour or two" after the specimens were collected.

In the present study, animals were observed on board the rowboat from which the collections were made, in the moment immediately after capture. All animals that were examined were then taken to the laboratory, about an hour and a half journey away, and re-examined. Nearly all of the stomach contents had been completely digested, and only the harder parts of the more resistent Cladocera remained. The major portion of even these hard parts had been egested, and had accumulated on the bottom of the container.

Crystal Lake is a small glacial lake just outside the city limits of Ravenna, Ohio. *Craspedacusta* previously has been reported from this lake by Dexter *et al.* (1949). These authors encountered it in large numbers in 1947 and in small numbers in 1948. Local fisherman claimed to have seen medusae every year for the previous nine years. It has been studied there since 1948 by Dexter (1954), and a detailed report is in preparation. In late September, 1954, the present author received reports of the occurrence of swarms of medusae from Mr. William E. Kelley, Director of the Cleveland Aquarium, who had collected a number of specimens for display purposes. The full cooperation of Mr. Kelley and of the entire personnel of the Cleveland Aquarium is gratefully acknowledged.

On the first day the lake could be visited (September 24), the number of medusae was greatly reduced, and they were found only at one locality, in contrast to their previously reported widespread abundance. However, 16 medusae were successfully captured by carefully dipping them out of the water with a finger bowl. The excess water then was decanted, the specimens observed with a dissecting microscope and the stomach contents enumerated. The results are shown in the accompanying table. The most abundant food organism was *Daphnia longispina,* with an average of 6.5 specimens per individual medusa. Next most abundant was *Diaphanosoma leuchtenbergianum,* with an average of 3.7 per individual (hence a total of 10.2 cladocerans per individual). The only other abundant food organism was the colonial planktonic rotifer, *Conochilus unicornis,* which averaged 2.6 colonies per individual. Among the copepods, *Epischura lacustris* was used only slightly, and *Cyclops* sp. hardly at all.

The present quantitative results confirm the qualitative findings of others, that the medusae of *Craspedacusta* utilize the plankton as food, though no evidence was obtained that phytoplankters are used. A plankton sample obtained at the time of the observations described above contained the same species of animals, and in somewhat the same proportional abundance, though there were relatively fewer *Daphnia longispina.*

TABLE I. *Stomach contents of medusae of* Craspedacusta sowerbii

Medusae No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Ave.
Conochilus unicornis (colonies)	1	1	2	14	1	0	1	8	4	0	3	0	2	4	1	0	2.6
Daphnia longispina	7	8	11	6	6	7	10	6	5	6	15	4	5	0	7	1	6.5
Diaphanosoma leuchtenbergianum	7	5	5	4	7	3	2	4	4	1	9	0	3	2	3	0	3.7
Epischura lacustris	1	0	0	0	1	2	0	0	2	0	0	0	1	0	1	2	0.6
Cyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0.06

From the above it is clear that the medusae of *Craspedacusta* compete directly with immature stages of game and other fish for their nutrition. Unfortunately, no reliable quantitative estimates of medusa number are available. At the point where the specimens for the above study were collected, it was subjectively estimated that there were about 3 specimens per m^3. Previous subjective reports by Dr. Dexter (personal communication), and in newspaper stories, indicated that there must have been, conservatively, at least an average of one specimen per m^2 of lake surface, considering the lake as a whole. Crystal Lake has been reported by Dexter *et al.* (1949) to have an area of about 101,200 m^2 (25 acres). From the fact that all food specimens were completely digested, and for the most part egested, at the end of 1½ hours, it can be conservatively estimated that a total of of 101,200 specimens were consuming 263,100 colonies of *Conochilus,* 657,800 *Daphnia,* 374,400 *Diaphanosoma,* and negligible numbers of other organisms every 2 hours, or approximately 3,157,000 *Conochilus,* 7,894,000 *Daphnia,* and 4,493,000 *Diaphanosoma* in 24 hours. These numbers are by no means excessive, but if there were 10 times as many medusae as were estimated, this would mean, assuming an average depth of 3-4 m, a destruction of 400-500 zooplankters/m^3/24 hours, which would be a significant quantity. Dexter *et al.* (1949) reported a maximum depth for Crystal Lake of 9.1 m (30 ft.). The fact that the competitive feeding of the medusae was relatively benign is indicated by the evident richness of the zooplankton at the time of this study, although no quantitative zooplankton estimates were made.

Furthermore, it is possible, as suggested by Dexter *et al.* (1949) that the medusae themselves are used as food by adult fish. Local fishermen have complained, both in 1947 (Dexter *et al.,* 1949) and in 1954, that the fish do not bite well when medusae are numerous. With the cooperation of the personnel of the Cleveland Aquarium, a medusa was placed in a small bowl containing a number of ordinary guppies. The fish attacked the coelenterate, and suffered no harm from the sting of the nematocysts. There was some evidence that the jellyfish was distasteful, or irritating, however. Larger fish perhaps would have found the medusae to be a convenient source of food.

SUMMARY

The food of medusae of *Craspedacusta sowerbii* was estimated quantitatively in the field at the time of capture. It was found that they were consuming primarily the zooplankters *Conochilus unicornis, Daphnia longispina,* and *Diaphanosoma leuchtenbergianum.* The daily consumption of zooplankters was appreciable, but not excessive.

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DIETARY PATTERNS OF RED AND GRAY FOXES

A more refined evaluation of differences in the adaptations of red (*Vulpes fulva*) and gray (*Urocyon cinereoargenteus*) foxes to their respective habitat niches, particularly as reflected in food coactions, is believed desirable. The following data are recorded as a means of suggesting some of the general points of variance in feeding trends where these foxes are found in the same area.

During the months of January, February and March of 1948, carcasses of 79 red foxes and 33 gray foxes were collected in Iowa. This sample contained carcasses of both species from each of 10 counties, largely in eastern Iowa. The processing of the carcasses in the laboratory included the identification of food remains in 45 stomachs and 69 intestines from red foxes and 19 stomachs and 26 intestines from gray foxes. The results are presented in Table I according to a technique of analysis described for food remains in fecal passages (Scott 1943) and later found useful in analyzing identifications of food remains from digestive tracts (Scott 1950).

Evidence of characteristic behavior and adaptation to habitat niche is reflected in the dietary patterns of these foxes taken in the same general area and in the same period of time. The most striking difference in the diets was in the proportions of plant foods. Plant remains occurred in markedly greater frequency and quantity in the stomachs and intestines of the gray foxes than in those of the red foxes. This tendency for plant foods to be noticeably more prominent in the winter diet of gray foxes was also evident in the findings of Nelson (1933), Errington (1935), and Hatfield (1939); however, attention was not directed to this difference. Further, the plant remains in the stomachs of the gray foxes had more the appearance of a staple winter food, for the foods, especially corn (*Zea mays*), had been more thoroughly masticated by the time they reached the stomachs (Fig. 1) than was the case for plant foods in the stomachs of the red foxes. The kernels of corn found in red fox stomachs were coarsely broken, if at all.

Although the difference in less striking, mammal remains tended to be represented more frequently in the diet of the red fox than in that of the gray fox. This, too, was evident in the data of Nelson (1933), Errington (1935), and Hatfield (1939). In this instance, the estimated proportion of mammal remains in the stomach and in the intestines of the red fox was roughly 1.5 times that for the gray fox. It was evident that the difference was brought about to a large extent by a greater representation of rodents, especially meadow mice (*Microtus*

TABLE I. *Occurrences of food remains in stomachs and intestines of red and gray foxes in Iowa*

Number containing food	Stomachs		Intestines	
	Red Fox 45	Gray Fox 19	Red Fox 69	Gray Fox 26
MAMMALS	66.2 (43)*	42.8 (18)	70.5 (67)	45.6 (21)
Undetermined	2.9 (2)	.....	2.0 (2)	.....
Determined	63.3 (43)	.....	68.5 (66)	.....
INSECTIVORES	1.1 (1)	1.7 (1)	4.4 (4)	.....
Blarina brevicauda	1.1 (1)	1.7 (1)	4.4 (4)	.....
RODENTS	34.8 (33)	20.5 (12)	56.5 (52)	22.0 (14)
Undetermined	6.3 (6)	6.8 (4)	3.4 (7)	10.3 (7)
Determined	28.5 (27)	13.7 (8)	53.1 (46)	11.7 (8)
Marmota monax	.....	1.5 (1)	.....	1.2 (1)
Geomys bursarius	0.8 (1)	.....	.....	.....
Reithrodontomys sp.	1.6 (2)	1.5 (1)	8.3 (10)	2.3 (2)
Peromyscus spp.	14.7 (18)	10.7 (7)	20.8 (25)	5.9 (5)
Microtus spp.	11.4 (14)	.....	24.0 (29)	2.3 (2)
RABBITS	25.3 (24)	20.5 (12)	38.0 (35)	23.6 (15)
Sylvilagus floridanus	24.2 (23)	20.5 (12)	36.9 (34)	23.6 (15)
Lepus townsendii	1.1 (1)	.....	1.1 (1)	.....
HOOFED MAMMALS	2.1 (2)	.....	1.1 (1)	.....
Sus scrofa	2.1 (2)	.....	1.1 (1)	.....
BIRDS	29.2 (19)	26.2 (11)	24.2 (23)	15.2 (7)
Undetermined	13.1 (9)	2.4 (1)	12.6 (12)	2.2 (1)
Determined	16.1 (11)	23.8 (10)	11.6 (11)	13.0 (6)
GALLIFORMES	13.2 (9)	11.9 (5)	8.4 (8)	6.5 (3)
Gallus gallus	8.8 (6)	9.5 (4)	6.3 (6)	6.5 (3)
Phasianus colchicus	4.4 (3)	2.4 (1)	2.1 (2)	.....
ANSERIFORMES	.....	2.4 (1)	.....	.....
Domestic duck	.....	2.4 (1)	.....	.....
PICIFORMES	.....	2.4 (1)	.....	.....
Colaptes auratus	.....	2.4 (1)	.....	.....
PASSERIFORMES	2.9 (2)	7.1 (3)	3.2 (3)	6.5 (3)
Undetermined	.....	2.4 (1)	2.1 (2)	4.4 (2)
Determined	.....	4.7 (2)	1.1 (1)	2.1 (1)
Cyanocitta cristata	.....	2.3 (1)	.....	2.1 (1)
Sturnella sp.	.....	.....	1.1 (1)	.....
Spizella arborea	.....	2.3 (1)	.....	.....
FISHES	.....	2.4 (1)	.....	2.2 (1)
Dorosoma	.....	2.4 (1)	.....	2.2 (1)
INSECTS	.....	.....	1.1 (1)	2.2 (1)
PLANTS	4.6 (3)	28.6 (12)	4.2 (4)	34.8 (16)
Zea mays	3.1 (2)	19.1 (10)	2.5 (3)	18.3 (10)
Carya sp.	.....	1.9 (1)	.....	1.8 (1)
Quercus sp.	.....	1.9 (1)	.....	1.8 (1)
Pyrus communis	.....	1.9 (1)	.....	3.7 (2)
Malus pumila	.....	3.8 (2)	.....	9.2 (5)
Prunus americana	.....	.....	0.8 (1)	.....
Vitis sp.	.....	.....	0.8 (1)	.....
Physalis sp.	1.5 (1)	.....	.....	.....

*First figure is per cent of total occurences; figure within parentheses is the number of occurrences.

FIG. 1. Well chewed corn from stomach of gray fox fills petri dish. This was the total contents of the stomach of a gray fox shot on February 6, 1948 and was typical of dry kernels masticated for food by this fox.

spp.), in the diet of the red fox. This is construed to have reflected prey availability because it is not thought likely that meadow mice would have been as common in the habitat niche of the gray fox as in that of the red fox.

Another difference inviting attention is the greater frequency of perching bird remains in the stomachs and in the intestines of the gray foxes than in those of the red foxes. This was also evident in Nelson's (1933) data.

It is believed that an appraisal of food habits based on a larger series of digestive tracts from both species or on an intensive investigation of the food habits of the gray fox in a measured environment would bring into sharper relief some of the departures of the gray fox diet from the better known dietary patterns of the red fox. And thus, a better understanding of the status of the gray fox as a predator would be realized.

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ANTS AND DERMESTIDS ON A MOUNTAIN TOP

Recent interest in the insect ecology of mountain tops (Chapman 1954a, 1954b, Dodge and Seago 1954) calls to mind observations made many years ago which may be worth placing on record. These concern the behavior of ants and dermestid beetles on the summit of Pyramid Peak, Dona Ana Co., southern New Mexico.

Pyramid Peak (Bishop's Cap Peak) is a more or less isolated pyramidal mass of fossiliferous limestone lying just southwest of the south end of the Organ Mountains, about 30 miles north of El Paso, not far south of Las Cruces. About its base are several smaller ridges of the same material, forming with it a small isolated range. It is on the east terrace of the broad valley of the Rio Grande about six miles east of the river. The plain on both sides of the river is approximately 1,300 meters above sea level, and the river has cut a very broad ravine through it to a depth of about 125 meters. The eastern escarpment of this ravine is eroded into a belt of low rounded hills. Above the level of the east terrace of the valley Pyramid Peak rises a little over 300 meters, most of this in great ledges of limestone produced by strata of different hardness. At the base it is surrounded by alluvial fans of limestone debris from its own slopes. On the east and north it is rather closely approached by fans of porphyritic alluvium from the Organ Mountains. The whole area is in the desert shrub formation. Fuller accounts of the area, especially of the plant communities, have been published previously (Fosberg 1931 and 1940) accompanied by maps.

As a member of a Los Angeles Museum expedition I was able to spend over two months in the vicinity of the Peak during the summer of 1930, during which time collections of plants and animals were made for the Museum. The curious set of ecological relationships described below was observed at that time. Another very short visit was made in August 1948 to see if the same phenomena were still observable. The construction of a beacon on the summit of Pyramid Peak had resulted in considerable alteration of conditions and it was only possible to repeat part of the observations at that time.

In 1930, on the actual summit of the peak, on and around the limestone boulders, were large numbers of the winged forms of one or possibly two species of ant. Two obvious forms were seen, one red with black abdomen, the other slightly smaller and entirely red. Closer observation of variability was not made. Some of these were in the act of mating. Sometimes several males were seen clinging to one female. As I remember it, mating was observed between all possible combinations: red and red, red and red and black, and red and black and red and black individuals, but I failed to record this in my notes. Between the rocks there were large quantities of remains of dead ants, probably mostly males that had died after mating or both sexes that had been killed by dermestid beetles and their larvae. There may have been a bushel or more of these. These were a few fragmentary remains of rabbits and coyotes (bones determined by H. A. Wylde) which had undoubtedly been brought there by golden eagles which were seen occassionally around the peak. There were hair, skin, and bones, and these were heavily infested by both larvae and adults of a medium sized dermestid determined as *Dermestis canerius* (Mannerheim) by D. W. Pierce (specimens preserved in Los Angeles Museum.) These

were also eating the ants, both dead and alive. The larvae were particularly voracious, seizing the ants by the tips of the abdomens and clinging till the ants were exhausted. Although the ants struggled they did not seem to be able to defend themselves.

The above observations were made on July 22. On September 6 another visit was made. There were still some ants of the same kind mating here, but in much smaller numbers. On August 15, 1948, the summit of the peak was revisited. As mentioned above, the site was much disturbed, but considerable numbers of ants were found mating, though not nearly so many as in 1930. A small platform had been constructed on the exact summit and most of the ants were crawling on this. As in 1930, the ants were of two colors, one red, the other black and red. Individuals of the black and red form were mating with each other, and were also attempting to mate with the red ones, though none successfully so far as observed. The red ones were much less active than the others. Both forms were collected and the lot was determined by M. R. Smith as probably *Pogonomyrmex californicus*. No dermestids were seen in 1948, but there were then no mammal remains and only small quantities of dead ants.

It is a pity that more adequate determinations cannot be made of the species of these ants. Collections were made both in 1930 and 1948. Those made in 1930 were unfortunately lost in the mail. The 1948 collection was given to Dr. M. R. Smith under the impression that it would be deposited in the U. S. National Museum. Recently I made an attempt to reexamine this collection more carefully to try to decide if one or two species were represented. I was informed that they had undoubtedly been discarded, as the Museum has neither space nor facilities for mounting any except collections of special interest. One wonders exactly how this is determined.

A. C. Cole (1954, p. 118) indicates that true *Pogonomyrmex californicus* Buckl. does not occur in New Mexico, but that a member of the "*Poponomyrmex californicus* complex" which he apparently regards as *P. maricopa* Wheeler occurs in the Las Cruces region. He further indicates that *P. barbatus* F. Smith, *P. desertorum* Wheeler, and *P. imberbiculus* Wheeler may also be found in this region. Dr. M. R. Smith (in conversation 1948 and 1954) says that at the present time it is impossible to determine with any certainty winged forms of *Pogonomyrmex* without accompanying workers. Dr. Cole (1954) reports that the populations of *P. maricopa, P. barbatus*, and *P. desertorum* in southern New Mexico are taxonomically very difficult, showing intergradation between different described species and subspecies and possible introgressive hybridization, at least within the several complexes represented. In view of this it would seem that specimens from the area, even those collected by ecologists, might be of more than passing interest.

In addition to the observations in Pyramid Peak others made in 1930 at several other points in the same area seem to have a bearing on the behavior of these ants. On July 28 similar ants were observed mating in considerable numbers on the crowns of isolated yucca plants on the summits of several of the low rounded hills along the east escarpment of the Rio Grande ravine. They were definitely observed to swarm around the yuccas, which were the most prominent elevations in the immediate vicinity, but were not seen in significant numbers elsewhere in the immediate surroundings. The ground was more or less covered, under the yucca bushes, by dead winged ants. When a tripod and planetable were set up here for surveying, the ants gathered around this and around the head of the operator to such an extent as to be quite a nuisance. On August 4 a visit was made to a windmill several miles south of this locality. The same ants were here in fair numbers around the windmill.

These observations, though isolated ones, seem to have some significance in relation to Chapman's summary of knowledge of swarming of winged ants around mountain summits in the western states (Chapman 1954b). He has several localities recorded in New Mexico, but none near Pyramid Peak. The genus *Pogonomyrmex* is not one of those recorded by him as swarming around mountain summits. Of particular interest is the support given to Chapman's conclusion that updrafts of air are not an adequate explanation of this behavior. The fact that the ants gathered around the yucca plants on slight eminences, around the head of the surveying instrument operator and his tripod, and around the windmill, as well as on the mountain summit, shows, I think, some sort of tropistic or instinctive behavior. Though one would certainly hesitate to ascribe a "purpose" to this, even in ants, it certainly seems that it must serve the function of encouraging cross-fertilization between ants of different colonies. If this attraction to high places is common to several species of *Pogonomyrmex* it may very well contribute to the variability and possible introgressive hybridization discussed by Cole (1954). Wheeler (1917, p. 178) describes swarming of two species of *Pogonomyrmex* but makes no mention of attraction to high places.

I do not know if predaceous behavior is known otherwise among Dermestidae, but the observations made on Pyramid Peak suggest either a facultative capacity for eating living prey or that this particular population had made a new discovery.

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REVIEWS

Elements of Ecology[1]

Here are some elements of ecology, physics, chemistry, plant physiology, animal physiology, pedology, oceanography and a little animal behavior (but no genetics). Perhaps ecology means a little of everything. The ecologist certainly sometimes feels like that and most definitions of ecology and environment are so broad as to provide justification for such an approach. On the other hand we may believe it is time that ecology (like genetics) decided to become a more definitive science, instead of being the poor relation borrowing from all. Some justification for this point of view can be found in the second half of the book. About 30 per cent of the first half is spent on analysis of what the author calls the physical environment; temperature, water, substratum, light and gases. This is a compendium of information which will be of great value to the ecologist who wants information on any of these subjects, as often he will. The rest of this half deals with the "biological effects" of these components of environment. For its relative brevity this seems sound enough, though Van't Hoff's law does not have the general application suggested on page 152 and a good deal more is known about photoperiodism in invertebrates than the statement on page 228 implies. In the second half of the book we meet plants and animals more frequently and perhaps the best of the book is saved for the last chapter on communities where the author seems thoroughly at home. In this half the chapters on population ecology are less satisfactory. The finite and infinitesimal rates of increase of a population are confused on pages 336 and 337. The finite rate of increase N_1/N_o on page 336 is not the same as the value "b" on the following two pages. In the equations on these pages "b"=antilog$_e$ N_1/N_o. The logistic equation has more restrictions on it than the statement at the bottom of page 340 presumes. Life tables deserve more than a passing reference in this section. The discussion on competition and predation is confused by failure to distinguish between these concepts. The section also suffers from an undefined use of "beneficial" and "harmful." These difficulties might have been overcome by introducing the concepts of chance to survive and chance to multiply. The transition from the brief discussion of competition and predation in experimental populations to what is supposed to happen in natural populations is a bit too slick to be convincing. More than elsewhere in the book, some of the "elements" of ecology in this section may turn out to have quite a short life. The chapters on community and productivity are particularly valuable and especially for the many references to freshwater and marine ecology. The approach here is fresh and stimulating. There is something wrong with the vegetation map of the world on page 450 which turns most of India into a "tropical forest" and gives none of this to Australia.

As a contribution to ecology this book has a twofold value. It makes a bold and quite successful attempt to present ecology and not just plant ecology or animal ecology. These two subjects are difficult enough to write on but the task of bringing together elements common to both plants and animals is immensely more difficult. Secondly the book brings together for the first time many examples from aquatic communities. This is its emphasis and in that it opens up new territory.

The dust jacket says "complex terminology is avoided" and this is a faithful statement. But we are not spared a superfluity of passive verbs and of generalities which amount to very little. We are told that "as a factor of environment the substratum is only slightly less elemental than the medium" that "temperature is perhaps the most commonly familiar ecological factor" that "nutrients are a crucially important influence" and so on. A little less of this would make for pleasanter reading. But these are minor faults and will not prevent the book from being accepted as a substantial contribution to the science and teaching of ecology.

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[1] Clarke, G. L. 1954. Elements of Ecology. xiv + 534 pp., 196 figs. New York: J. Wiley and Sons. $7.50.

Climatic Environment[1]

If the adjective comprehensive were used to begin the title of this book its content would be even more precisely indicated. The author, S. S. Visher, is eminently qualified by inclination, temperatment, and previous work in this field to undertake the project of preparing such an atlas and advancing it to this successful conclusion. He gives his sources in a "References" section at the end of the volume. From this detailed list one gets the impression that as each new paper or book relating to the climate of the United States appeared it was avidly seized upon by our author and its contribution to the over-all survey here presented carefully abstracted and adapted to the purpose. The 600 maps so obtained are supplemented by 400 original with the author.

There is a Foreword by Charles F. Brooks of the Blue Hill Meteorological Observatory which makes clear the place of this book in relation to previous publications covering the same ground. This foreword contains a statement, significant to the ecologist, to the effect that the data on which the maps are based are mostly from stations in cities and in valleys rather than on mountains. This circumstance, accordingly, should be borne in mind when it is sought to evaluate the climatic environment of a highland site, within a general region, by study of the map. Since adjustments for the altitude

[1] Visher, S. S. 1954, Climatic Atlas of the United States, xii + 403 pp. (large quarto), 1031 maps and graphs, Cambridge, Massachusetts: Harvard University Press. $9.00.

factor, at least for temperature, can be made with relative ease and assurance the general worth of the Atlas for analysis or interpretation of the climatic environment of an organism is not basically affected.

In this connection it should also be noted that the maps have been, in general, simplified and reproduced on a uniform scale. This greatly facilitates an "at a glance" survey of all the factors applying to a given region or discovering how a particular factor is operative in a region as related to its incidence in adjoining or remote regions.

It might be thought that such simplification could significantly reduce the accuracy of the representation. This does not appear to be the case. A check on a number of the maps *in re* their conformance to climatic conditions in a region with which the reviewer has been familiar for a period of 40 years indicates a surprisingly marked agreement between mapping and experience.

A sampling along other lines proved interesting. The reviewer recently sought information on wind strength, direction, and steadiness on the Great Plains and found only vague accounts. Figures 377-390 in the Atlas afforded specific data on the directions and average force of the winds but nothing on the constancy, duration, or extremes of velocity. In other words there was nothing in the maps to confirm a popular conviction that inhabitants of the Great Plains have to *endure* long periods of unremitting high winds. Perhaps this concept is only specious folklore.

Maps 325-327 show the average and extreme depth of frost penetration into the ground. Here one looks for a map of stable ground water temperatures below the zone of seasonal fluctuations, but none is provided. One may assume, of course, that this constant temperature will correspond to that of the average annual air temperature of the place but a confirming map, observationally based, would be reassuring, especially as, in a region known to the reviewer, the ground water temperature is considerably higher than the average annual air temperature.

Readers who are persuaded that "winters are not what they used to be" will find the climatic change maps 1008-1012, 1024-1025, 1029-1031 and graphs 1013-1023, 1026-1028, an interesting study. On page 17 there is a nice summary of the effect of the Great Lakes on climatic elements.

The captions and legends on the maps are concise, in some cases to the degree of being cryptic. Since the format provides ample room for much more extended descriptions it is regrettable that this space was not used for interpretative matter to indicate the significance of many of the representations. Map 40 shows the difference in normal temperatures between February and December (February minus December). Presumably this represents how much colder, on the average, February is than December. What pertinence does this have? Map 212, "temperature efficiency" needs further elucidation. The caption for map 213, cold degree days is definitely cryptic. The numbering on maps 582-589 "normally driest periods" requires further explanation. Captions on maps 886 and 887 appear to be transposed. There seems to be an extraordinary lack of correlation in parts of graph 928.

The Harvard University Press has provided a handsome format and typographic dress. This is slightly marred by what appears to be an unfortunate transposition of section heads and page captions of Sections 27 and 28, Frequencies of Wet Years, Seasons, and Months and Frequencies of Dry Years, Seasons and Months. Again, pages 237-243 are designated Normal Amount of Snowfall whereas hail, excessive rains, prospects of rain are somewhat incongruously dealt with. The lettering of map 980, and the numbering of Climatic Regions maps 973-978, 983, 986-987, 1001 are so faint as to be almost illegible.

However, these textual and typographic defects are only minor blemishes of an imposing, well organized, and extraordinarily useful reference work on the climate of the United States. The author has, as he states was his purpose, "mined" the accumulated statistical data with assiduity and beneficiated the ore with much success.

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An Illustrated Regional Flora for the Upper Ohio River Basin[1]

This quarto two-volume set is such a fine combination of science and art that it stands unique among regional American floras. Far from being merely a collection of superb wild flower paintings as might be indicated by the somewhat misleading title, it is a solid scientific work in which the brilliant watercolor plates serve as illustrations for the well-written text. It is a flora of a limited region done so thoroughly and meticulously that it stands almost in a class by itself.

The text, which makes up Volume I, is the result of over fifty years of botanical investigation in the region of the upper Ohio River Valley by Dr. Jennings, long a well-known member of the Ecological Society. As delineated by the author, this region consists of western Pennsylvania, southwestern New York, eastern Ohio, northern West Virginia, and western Maryland. This is an area of varied topography in the northern part of the deciduous forest formation and contains most of the species characteristic of that formation.

A total of 2,260 species, 437 varieties, and 104 forms of native and introduced seed plants are described, with detailed notes on the distribution of each of these taxa in the upper Ohio Basin. Collection maps are presented for 146 species because of their rarity or distinctive distribution patterns in the region. Keys to families, genera, and species seem clear and well-written.

The introduction, entitled "The Botany of the Region" will be of particular interest to ecologists. It presents a history of the botanical work in the area from the visit of Peter Kalm in 1750 up to the collectors of the present time. A large part of the introduction is devoted to sections on the general environments of the region. These introductory chapters include a section on geology and soils, one on physiography and topography, and another on climate. Finally, an interesting summary of the plant

[1] Jennings, O. E., and Andrey Avinoff. 1953. Wild Flowers of Western Pennsylvania and the Upper Ohio Basin. 2 volumes. Vol. I, lxxv + 574 pp., 150 maps; Vol. II, xvi + 200 plates. Pittsburgh: University of Pittsburgh Press. $60.00.

geography traces the development of the flora and vegetation from early Tertiary times up to the present. This latter section also describes the principal plant community types, while lists of species which are characteristic of, or restricted to, particular regional habitats are also given.

The descriptions of the taxa are clear, complete, and have a high degree of accuracy. It is a pleasure to see the names of authorities spelled out instead of the usual abbreviations. Citations to monographic treatments and papers dealing with critical taxa are given with the descriptions, where such references are most useful.

The greater part of the text conforms to the International Code of Botanical Nomenclature as revised at Stockholm in 1950. Before these new rules were available, however, the text had already been printed up to p. 168. Beyond that point, the author changed nomenclature and descriptions to conform with the revised code. An appendix lists nomenclatorial changes in the first 168 p. which are needed to conform to the spirit of the revised rules. The changes, particularly those incorporated in the text from p. 168 on, required much effort and time with a consequential delay in the publication date. However, they do add considerably to the potential value of the book as a technical source.

With the descriptions are detailed notes on the occurrence of each taxon within the limits of the upper Ohio Basin. The treatment is classical throughout and no new taxa are described. A complete bibliography, a gazetteer of the region, and a glossary make this volume even more useful.

Volume II is made up entirely of plates. These are reproduced from watercolors by the late Andrey Avinoff, who was, from 1926 to 1945, director of the Carnegie Museum of Pittsburgh. There are 200 of the plates illustrating 253 plants. The paintings, which were done from living specimens, are of great delicacy and beauty; they will rank among the best that have been done anywhere. For the professional and the amateur alike, they are not only works of art but are technically accurate illustrations. This is no surprise, since Dr. Avinoff was a scientist as well as an accomplished artist. The reproductions are brilliant, lifelike, and faithful to the originals. The plants are all shown natural size with occasional insets of larger magnification. A short, nontechnical description and collection data concerning the actual specimen accompany each plate.

Nothing, apparently, was spared to make the set perfect throughout. The type face is large, clear, readable, and attractive. The sheet-fed gravure technique of reproducing the watercolors has had excellent results. The paper was especially made for the set and is of 70 pound weight in Volume I and 90 pound weight for the plates in Volume II. Each plate is protected by a sheet of linen bond.

While the initial cost of this set will appear high to the average ecologist, it is really somewhat of a bargain since the actual cost of production of the limited edition of 3,000 sets was considerably more than 60 dollars per set. The publication in this form was made possible by a generous grant from the Buhl Foundation of Pittsburgh.

This work by Jennings and Avinoff will long remain a scientific and artistic classic in the field of regional floras.

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The Social Behavior of the Herring Gull[1]

The aim of this book, according to the author (p. xvi), is not to give an exhaustive treatise of Herring Gull sociology, but rather to attempt a sketch of the problems as he now sees them. Most of the many facts contained in this useful book have been published before in various articles and other books by Tinbergen, and are here brought together in convenient form to give something of an over-all picture of the life of one species of bird.

The method of study consisted primarily of field observation with binoculars by a more or less hidden observer, and was often supplemented by field experiments. Individual birds were recognized by plumage peculiarities and other cues; during one year 14 gulls were also given colored leg-bands. The author names ten students and field companions who have aided him in the field work over the years.

The main substance of the book is a detailed and theoretical analysis of reproductive behavior in the Herring Gull (*Larus argentatus*). Many aspects of the different postures involved are illustrated by line drawings often taken from films, and by a series of magnificent photographs. In sequence Tinbergen describes and analyzes the arrival of the birds at the breeding site, fighting behavior and threat displays, territorial behavior, pair-formation, copulation and courtship displays, nest-building, incubation, egg recognition, hatching and parental care of chicks, and the behavior of the chicks with special reference to social signals and personal ties with the parents.

The detailed table of contents seems to suffice as a subject index. The book has an index to authors and to species of birds and other animals mentioned in the text. There is a bibliography of six pages, and the literature citation, admittedly incomplete, leaves some important gaps. For example, there is no mention of any of the various published reports on the endocrine control of breeding behavior in gulls. Near the end of the book there is a chapter on "Sign stimuli in other animals" that seems somewhat irrevelant.

The style of presentation generally is clear, interesting, logical, keenly imaginative, and basically objective. The author emphasizes (p. 156) the importance of avoiding anthropomorphic terms in the description of a bird's behavior.

The adult Herring Gull has a red spot on each side of the lower mandible, and the function of this red spot seems to be to stimulate and direct the feeding responses of the recently hatched chick. By an ingenious series of models the author and his students have gathered evi-

[1] Tinbergen, Niko. 1953. The Herring Gull's World. A study of the social behaviour of birds. xvi + 255 pp., 58 figs., 30 plates. London: Collins Clear-Type Press, New York: Frederick A. Praeger. $4.00.

dence that color, background contrast, position, and movement of this spot are all important elements in stimulating the chick to peck at the beak of the parent and thus be guided to the food which is normally held in the beak when the parent feeds its young. This series of experiments represents the climax and most original contribution of the book, and provides one of the best analyzed examples we have at present showing the function of any type of bird coloration.

However, even this case does not seem entirely satisfactory. The results are presented in graphical form showing the number of pecking responses to the models with no indication as to number of individual chicks involved for each test. In none of the tests, as described in this book or in the published articles on which it is based, were statistical tests of significance applied to any of the differences secured. Furthermore, although one may have confidence in the skill and impartiality of the experimenters, the latter themselves gathered evidence to show that not only movement, but also lowness, nearness, and the angle at which the model of the parent's beak is held are important in stimulating the pecking reactions of the chick. These are all conditions conceivably liable to sub-conscious and subjective influence during successive presentation of hand-held models. In general, the evidence which is reported in this book in support of various conclusions is presented in a plausible and logical manner, but this evidence often needs to be strengthened and amplified to be thoroughly convincing. This is not to ignore the stimulating value of the theoretical framework and its value for further research.

Indeed, the author seems to be well aware of present limitations of the study. This book is apparently intended as a progress report for the general reader, and the statement is made in the concluding chapter that "The main result of our Herring Gull work therefore is not to be found in the conclusions drawn, but rather in the sharper formulation of the problems."

It is encouraging to know that both in Europe and America, various students are taking up the study of other species of gulls and terns. Not the least of Tinbergen's contributions to animal sociology has been the inspiration he has afforded to students interested in the behavior of animals under natural conditions.

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ENVIRONMENT AND EUROPEAN HISTORY[1]

Professor Whittlesey prepared the manuscript of this book in response to a request of his colleagues teaching history at Harvard University that he provide a book of outside readings, as it were, for a general course in European history. Whittlesey has always been actively interested in history, and this volume is living proof of the close relationship that geography and history bear to each other.

"Environmental Foundations of European History" will be called historical geography by those engaged in the profession of geography, perhaps the historians prefer to label it geographical history. In either case, it provides an excellent short introduction to the geographic background against which history has to be viewed, if it is not to remain, in the words of Captain John Smit, "a vagrant without a certaine habitation."

The author approaches his subject under four principal headings, each corresponding to a major era of European history. After a brief introductory statement, giving Europe its proper setting in the wider framework of Eurasia, and a general reference to the "anterooms of European history" in the eastern Mediterranean, four main chapters trace the geographic background of Europe's state of development. The first of these describes Europe on the threshold of the Middle Ages; the second deals with Europe on the threshold of the Discoveries; the third treats Europe on the threshold of the Industrial Revolution; the fourth, Europe on the threshold of tomorrow. Viewed by a geographer, it might be said that these chapters describe Europe in terms of the increasing sphere of European action; Europe and its immediate surroundings on the threshold of the Middle Ages; Europe about to embark on the great adventures of exploration and discovery that began with the Portuguese voyages; Europe on the threshold of the Industrial Revolution that was, for the brief span of a century, to make Europe the principal purveyor of manufactures for the entire world; and Europe today, facing its greatest crisis in a world that is challenging European supremacy.

The approach used by Professor Whittlesey is one all too rare in American literature that is sadly deficient in works of this type. Perhaps the facts here enumerated are elementary, perhaps there is a tendency to simplifying the great and complex process of interaction between man and his environment. These are very minor criticisms, however, for the author succeeded in building a firmly founded and harmoniously proportioned framework of geographical facts upon which the American college student, usually deficient in the most elementary knowledge of geography, can readily base his own readings of history.

The maps accompanying "Environmental Foundations of European History" are well designed, and the short bibliographical appendix will prove most useful to students interested in becoming acquainted with the basic works of geography bearing on this subject.

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[1] Whittlesey, D. 1949: Environmental Foundations of European History. xvi + 160 pp. Illus. New York, Appleton-Century-Crofts. $2.25.